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1.—General view of the bog, looking northwards to the hills beyond Loch Maree. (C.f. Photo 282, Plate 115, Tansley, 1939.)
2.—Pool and flats in centre of the bog.
3.—An early stage in the development of a *Rhacomitrium lanuginosum* hummock.

TRANSACTIONS
OF THE
BOTANICAL SOCIETY OF EDINBURGH

SESSION CXXIV

The Ecology of a small bog in Kinlochewe Forest, Wester Ross.

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I. Introduction.

In *The British Islands and their Vegetation,* A. G. Tansley (1939) drew attention to a bog, "completely enclosed by native pinewood on the south-western side of Loch Maree in Ross-shire". Giving a short description, flora list and sketch-map of the bog, he referred to these as "the only available description of a Scottish raised bog" of which it was regarded as "a small but very perfect example". The area now forms part of the Beinn Eighe Nature Reserve, and our attention was drawn in 1955 by Dr. D. N. McVean, then Senior Scientific Officer in the Nature Conservancy, to a site towards the eastern limit of the wood which, he believed, after careful search, to correspond to that described by Tansley. This was a subject of investigations in the summers of 1955 and 1957 by members of Field Classes from the Aberdeen University Botany Department. Detailed comparisons were made with Tansley's description and his photograph (plate 115), which, in spite of changes in the profile of the adjacent forest, provides a reference to the outline of hills beyond (see Photo 1). After renewed search of the neighbourhood it was concluded that this site alone showed agreement in all respects.

However, certain aspects of the description and in particular of the sketch map (admittedly prepared "from memory"—see caption to Fig. 684, Tansley, 1939) did not correspond fully with

the features of the bog as observed in 1955, nor was the impression of it as a "very perfect example of a raised bog" easy to sustain. Indeed, Durno and McVean (1959) in a brief reference to it state that it "has been erroneously described as a raised bog by the late Sir Arthur Tansley (Tansley, 1939)". Further detailed studies of raised and other bogs in Scotland (Pearsall, 1956; Ratcliffe and Walker, 1958) are now available, and it may therefore, be of interest to place on record certain aspects of the ecology of the bog in Kinlochewe Forest.

The area of the bog is only about 12,000 sq. m., its outline being approximately oval and measurements about 150 m. × 80 m., the long axis running N.-S. It lies about 45 m. above the level of Loch Maree, and, according to Durno and McVean (1959), is situated in the shallowest of a linear series of morainic basins. The rim of this basin forms the northern and eastern margins of the bog, to the south and west the bog surface merges gradually into the up-slope of the hill (Fig. 1). A stream descending the hill reaches the S.W. extremity of the bog and feeds some water into it, turning *E.* (cf., however, Tansley's sketch map) and continuing for a time round the edge where it receives a certain amount of drainage water from the bog. Although in this S.E. part there is some resemblance to a "lagg", the stream later drops away over the edge of the basin and, thereafter, has no connection with the bog. On the W. side there is no boundary stream receiving drainage from a higher bog surface; on the contrary, several minor channels from the hillside feed into the bog. Thus water enters more or less continually from the W. and S.W., moving slowly through and draining out mainly at the north-east end where the margin of the basin drops away towards Loch Maree, also to a lesser extent at the E. and S.E. margins.

Along its eastern side, the rim of the bog is rather distinct, dropping fairly steeply down to the surrounding soil-level of the openly wooded hillside. The impression of a "rand"* is thus readily created, especially as this part supports a tall *Calluna* community with moderately well-developed Pine trees. However, as will be shown, this is in fact not the margin of a convex peat-formation; but a raised rim bordering a more or less concave peat surface.

*Tansley, however, did not use this term, referring simply to a "marginal *Calluna* zone".

The bog surface presents a pattern with three chief components:

(i) The pools and channels (photo 2), which account for about 37% of the surface area. The most extensive channels lie towards the centre of the bog parallel with its long axis, formed presumably in accordance with the main directions of water flow. Some branches from these and lines of pools extend towards the E., representing the direction of minor outflows; two channels running W.-E. enter the bog near its N.W. corner and can be observed to be inflow channels. Smaller pools of irregular shape are scattered throughout the centre of the bog.

(ii) Level surfaces normally just above the water table (photo 2), of the kind termed 'flats' by Ratcliffe and Walker (1958). These surfaces, occupying about 41% of the area, lie not more than about 15 cm. above the water table and support a vegetation comparable with that described by Sjörs (1948, 1950*b*) as fen 'lawn'.

(iii). Hummocks (photos 3 and 4), interspersed in the flats, covering the remaining 22% of the area. These are of various shapes, rounded, oval or elongate, lacking any obvious uniformity of orientation. Only a few are composed entirely of *Sphagnum* spp.; the majority, including all the large ones, consist mainly of *Rhacomitrium lanuginosum*. In many cases the *Rhacomitrium* hummocks are founded on pre-existing *Sphagnum* hummocks, others have as a basis an old tree stump, a stone or a former tuft of *Eriophorum vaginatum*. In Tansley's account the hummocks in the southern half of the bog are regarded as representing an active "regeneration complex", a view which will be discussed later; "rocky outcrops" in the centre were also mentioned, but unless the reference applied to a few groups of large coalesced hummocks possibly founded on boulders, these were not traced in the present survey.

Pine seedlings and dwarf trees of various ages "in check" are numerous, both on hummocks and flats, but in the bog none has developed into a full-grown tree.

With the aim of reaching some conclusion on the processes of bog formation at work here, data were obtained on the following features: depth and configuration of underlying mineral basin; depth and surface topography of peat; peat stratigraphy; vegetation and hummock construction; and the pH and conduc-

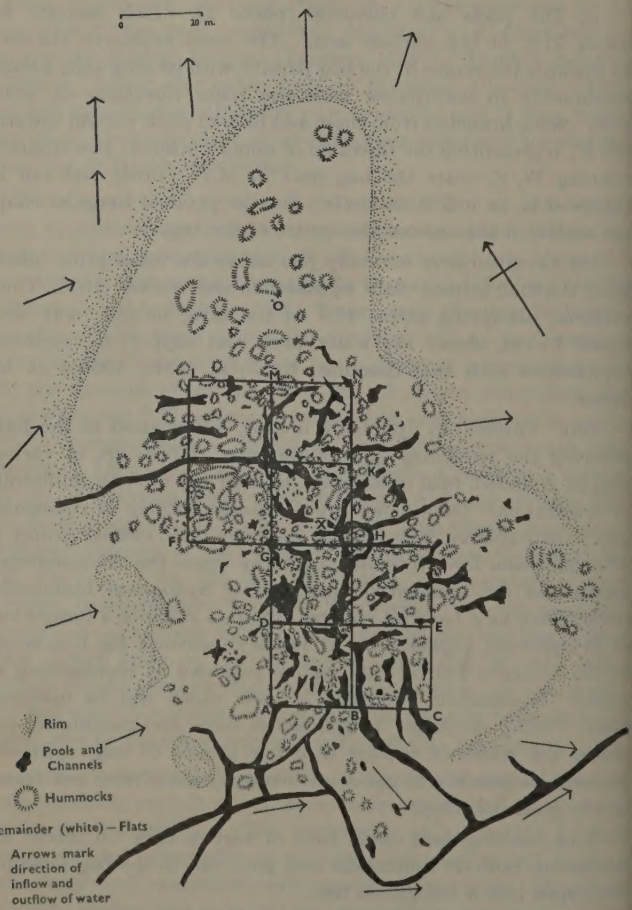


FIG. 1.—General map of the bog showing pools, flats and hummocks, and the position of the marked squares and points.

tivity of water from various parts of the bog in comparison with inflow and outflow channels.

II. THE MINERAL BASIN AND OVERLYING PEAT.

After an initial survey, a grid of eight 20 m. squares was delineated from a base line lying parallel to the long axis of the bog (Fig. 1). The points formed by the intersections of the grid were levelled on to the point A; peat depths were recorded at the same time. A further series of peat depth measurements and levellings* was made in two concentric circles around point X (Fig. 1) at the centre of the bog. An inner circle of seven points fell within the boundary of the bog proper; an outer circle of nine points was described upon the rim.

From these measurements it was possible to construct a contour map of the mineral basin which is concealed by the overlying peat (Fig. 2). This gives a clear indication that the bog has formed in a saucer-shaped depression with an elongated lip sloping away to the north-east, but rising fairly sharply to the rim on the east and west sides and more gradually again towards the south, thus giving the bog its elongated shape. The downhill slope towards the north-east provides the main exit for drainage water. The "floor" of the bog consists of a tightly packed mass of gravel and stones.

The contour map of the peat surface (Fig. 3) exhibits a similar trend, the rim being raised above the general level of the bog which slopes at first gently, and then more steeply from south to north. Fig. 4 shows a number of transverse and longitudinal sections of the bog from which a clearer picture of the variation in peat depth in relation to the configuration of the mineral "floor" may be gained. The deepest peat occurs at the northern end of the bog and the shallowest at the southern end and towards the eastern and western perimeters.

Clearly this bog does not conform to the classical convex shape of typical raised bogs such as has been described for Tregaron Bog in Cardiganshire by Godwin and Conway (1939). It is markedly concave, the peat surface at the centre being some 40 cm. below that at the east, south and west margins of the bog.

*Levelling was approximate only, carried out by means of an Abney level.

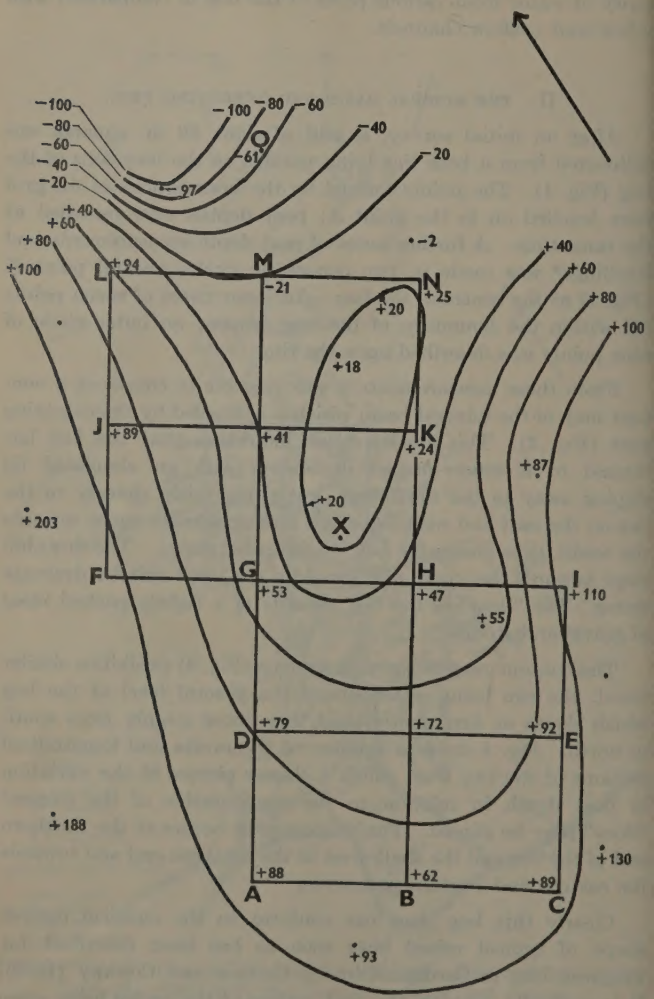


FIG. 2.—Approximate contour map of the underlying mineral basin. Figures show differences in level above (+) or below (−) point X.

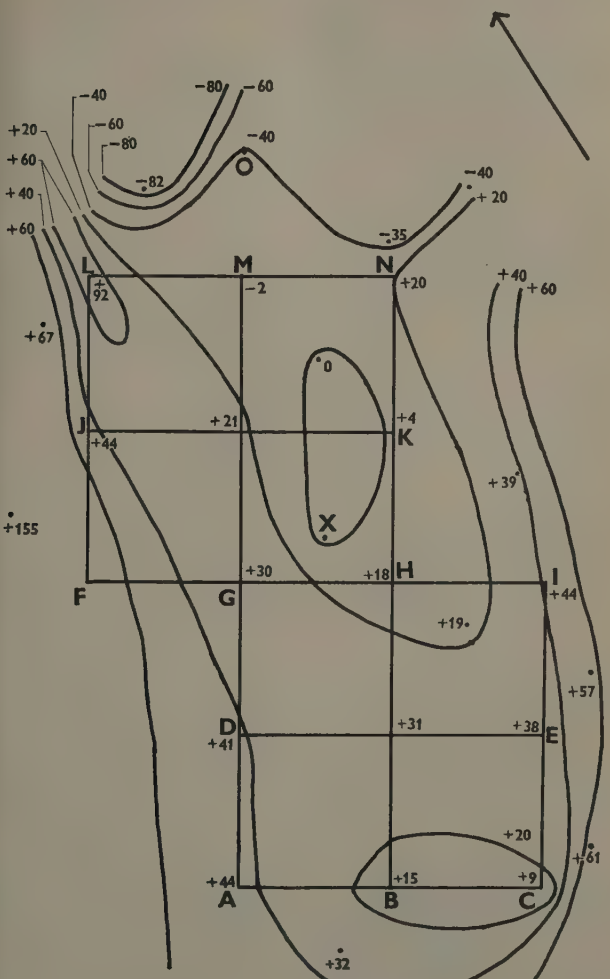


FIG. 3.—Approximate contour map of the peat surface. Figures show differences in level above (+) or below (–) point X.

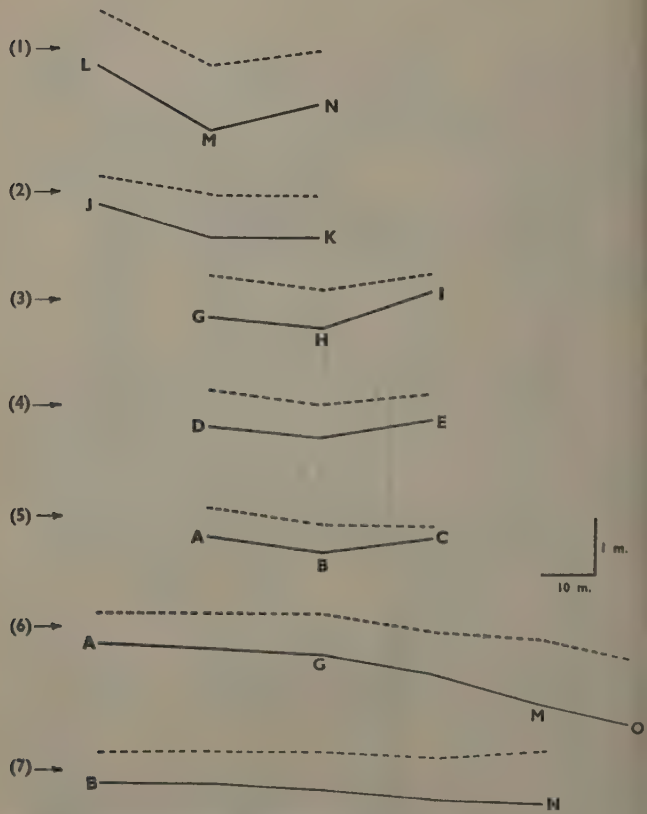


FIG. 4.—Representative sections. (Broken line—peat surface; continuous line—underlying mineral basin.)

Nos. 1-5. Sections across the bog; arrangement corresponding to position in Figs. 1-3.

Nos. 6 and 7. Sections along the length of the bog.

The depth of peat is nowhere great, varying between about 30 and 120 cm. Detailed stratigraphical analysis has not been attempted, but several pits were dug through the peat in various parts of the bog, down to the mineral basin. All of these showed the same gross profile features, and the following serves as a typical example, taken in one of the flats: —

Surface	Fibrous brown peat, with matrix of *Sphagnum* containing remains of *Eriophorum angustifolium, Scirpus caespitosus* and *Molinia caerulea.*	Top 10 cm. darker, perhaps marking zone of fluctuation of present water table and periodic aeration.
30 cm.	Soft amorphous peat, readily squeezed through the fingers, dark red-brown. Many roots; and towards base, roots, twigs, portions of branches and occasional stumps of birch.	
50 cm.	Dense black layer, apparently charcoal, similar in appearance to a layer lying just above the A_2 horizon of the podsol under the neighbouring pine wood.	
54 cm.	Mineral "floor"—stones of assorted sizes.	

From this simple stratigraphy several points emerge.

(i) Following a previous vegetation, perhaps destroyed by fire, the first peat-forming communities of the site were of a swampy birch-wood character, and the bog probably did not originate in an aquatic or poor-fen type of vegetation (as in many raised bogs).

(ii) The uniform nature of the upper 30 cm. or more of peat, lacking recurrent strata of particular species or lens-shaped masses of *Sphagnum,* indicates steady peat-formation over a considerable period by vegetation substantially similar to that of the present-day flats. Evidence for active vegetational cycles or "regeneration complex", as associated with certain raised bogs, is lacking, and the hummocks of the present bog surface may be relatively recent developments.

(iii) The dark upper layer of peat may suggest a tendency towards some drying of the surface, a conclusion perhaps supported by the frequency of *Calluna* in flats and hummocks of the present-day vegetation, and similarly of *Rhacomitrium* in the hummocks, in contrast to the scarcity of their remains in the peat.

All these stratigraphical features bear a marked similarity to those described for the Silver Flowe bogs by Ratcliffe and Walker (1958).

III. VEGETATION.

THE STREAM AT THE S. MARGIN. Since attention was concentrated on the bog surface, only scattered observations were made in the marginal regions. The following list, however, was obtained from the sides of the stream skirting the southern edge of the bog:

Calluna vulgaris
Erica tetralix
Blechnum spicant
Molinia caerulea
Carex echinata
Scirpus caespitosus
Narthecium ossifragum
Drosera anglica
D. rotundifolia
Pedicularis sylvatica
Polygala serpyllifolia
Potentilla erecta
Succisa pratensis
Breutelia chrysocoma
Hylocomium splendens
Sphagnum spp.
Thuidium tamariscinum

ELEVATED MARGINS AND RIM. The rim of the bog on the east side and the gentle up-slope to the west are sparsely wooded with pine trees, set in a *Calluna*-dominated community. This contains seedlings of *Sorbus aucuparia* and *Betula pubescens*, also appreciable quantities of *Vaccinium myrtillus, Myrica gale* and *Pteridium aquilinum*. Mosses include *Dicranum scoparium, Hylocomium splendens* and *Rhytidiadelphus loreus*.

THE BOG SURFACE. In the eight marked squares in the central part of the bog the distribution of pools, flats and hummocks was mapped in detail, while somewhat less accurate sketch maps were prepared of the surrounding portions. From these, the map shown in Fig. 1 was prepared. In each of the marked squares the communities were examined as follows. Species lists, with an estimate of cover according to Braun-Blanquet's cover-abundance scale, were made from five pools or channels where the summer water table stood above the peat, from five 1/10 sq. m. quadrats on the flats, and from at least three hummocks. (In the case of

hummocks, separate lists were made from the margins, sides and tops.) In this way, totals of 40 pools (of somewhat varying size), 40 quadrats on the flats and 28 hummocks were examined; Table 1 gives the frequencies of the species in these samples, together with the means of the figures recorded for each on the cover-abundance scale.

TABLE 1.

FREQUENCY AND COVER OF SPECIES IN SAMPLES OF POOLS, FLATS AND HUMMOCKS.

(For details of sampling, see p. 134.)

Columns headed 'F' show frequency on a 5-point scale os follows:— 5: 80-100% occurrence; 4: 60-79%; 3: 40-59%; 2: 20-39%; 1: 1-19%.

Columns headed 'C' show mean values for cover-abundance on the Braun-Blanquet scale.

	POOLS		FLATS		HUMMOCKS					
					Margins		Sides		Tops	
	F	C	F	C	F	C	F	C	F	C
Tree Seedlings										
Betula sp.	·	·	1	+	·	·	·	·	·	·
Pinus sylvestris	·	·	·	·	1	+	·	·	1	+
Dwarf Shrubs										
Calluna vulgaris	1	+	4	1	5	2	5	2	5	2
Erica cinerea	·	·	1	+	·	·	·	·	·	·
E. tetralix	5	1	5	2	5	1	5	1	2	+
Myrica gale	1	+	1	+	1	+	1	+	1	+
Grasses										
Molinia caerulea	2	+	5	+	5	2	5	2	5	2
Sedges and Rushes										
Carex echinata	1	+	1	+	2	+	1	+	1	+
C. panicea	1	+	1	+	1	+	1	+	1	+
Eriophorum angustifolium	5	1	4	1	5	1	5	1	5	1
E. vaginatum	·	·	5	2	5	2	5	1	4	1
Juncus squarrosus	·	·	1	+	·	·	·	·	·	·
Rhynchospora alba	5	1	2	+	1	+	·	·	·	·
Scirpus caespitosus	·	·	3	1	3	1	2	+	1	+
Other Monocotyledons										
Narthecium ossifragum	2	+	4	1	5	1	4	1	2	+
Potamogeton polygonifolius	1	+	·	·	·	·	·	·	·	·

*The Braun-Blanquet cover-abundance scale is as follows:—

5: covering more than ¾ of the area.
4: any number of individuals covering ½-¾ of the area.
3: any number of individuals covering ¼-½ of the area.
2: very numerous or covering at least 5% of the area.
1: plentiful, but of small cover value.
+: sparsely or very sparsely present, cover very small.

Dicotyledonous Herbs										
Drosera anglica	3	1	1	+	1	+	·	·	·	·
D. rotundifolia	1	+	5	1	5	1	2	+	1	+
Pedicularis sylvatica	·	·	2	+	2	+	·	·	·	·
Pinguicula vulgaris	·	·	1	+	1	+	·	·	·	·
Polygala serpyllifolia	·	·	1	+	1	+	1	+	1	+
Potentilla erecta	·	·	3	+	5	1	4	1	2	+
Mosses										
Dicranum scoparium	·	·	·	·	1	+	·	·	·	·
Hylocomium splendens	·	·	·	·	1	+	·	·	·	·
Hypnum cupressiforme	·	·	1	+	1	+	1	+	1	+
Rhacomitrium lanuginosum	·	·	1	+	5	2	5	4	5	5
Sphagnum cuspidatum	5	5	2	+	2	+	1	+	·	·
S. subsecundum var. auriculatum			·	·	·	·	·	·	·	·
S. papillosum	1	+	5	3	5	2	2	+	1	+
S. rubellum	·	·	2	+	5	1	2	+	1	+
Hepatics										
Cladopodiella fluitans	3	+	·	·	·	·	·	·	·	·
Pleurozia purpurea	·	·	4	1	4	1	2	+	1	+
Lichens										
Cladonia spp.	·	·	1	+	5	1	4	1	3	+

Species recorded in the bog, but not included in the samples:—

Pools and wet hollows
Juncus kochii
Sphagnum palustre
Cephaloziella hampeana
Gymnocolea inflata
Mylia anomala
Odontoschisma sphagni

Flats
Sphagnum magellanicum
S. plumulosum
S. tenellum

Hummocks
Campylopus atrovirens
Tetraplodon mnioides (on owl's pellet)
Lepidozia setacea

Pools.

Almost all pools and channels, irrespective of size, are filled with a dense cover of one or both of two *Sphagnum* species, *S. subsecundum* var. *auriculatum* and *S. cuspidatum*. Other species of high frequency are *Eriophorum angustifolium* and *Rhynchospora alba*, while *Erica tetralix* and *Drosera anglica* are more scattered.

Sphagnum subsecundum var. *auriculatum* tends to occupy the centre of the deeper pools while *S. cuspidatum* occurs in the shallower parts. The two species frequently occur mixed, but the shallower pools may contain *S. cuspidatum* alone. Where most of the *Sphagnum* mat is submerged under some depth of water numerous shoots are also often found floating at the surface.

Eriophorum angustifolium grows up through the standing water of the deeper pools but *Rhynchospora alba* is more frequent in those of medium depth, while *Molinia caerulea, Carex echinata* and *Erica tetralix* belong to the margins or shallow pools. Where the *Sphagnum* species are unhealthy, often in shallow water, they are frequently overgrown by large quantities of *Cladopodiella fluitans.* Species characteristic of flats reach the edges of pools, e.g. *Sphagnum papillosum, Narthecium ossifragum, Molinia caerulea, Erica tetralix, Drosera rotundifolia.*

FLATS.

The vegetation of the flats is rather uniform, constituting a regular, rather dense turf, of which the basis is formed by *Sphagnum papillosum. S. cuspidatum* is also present, but *S. subsecundum* does not enter this community. The following species have high frequency and all contribute significantly to the vegetational cover:—*Molinia caerulea, Eriophorum vaginatum, Narthecium ossifragum, Erica tetralix*; prominent in the bryophytic stratum is *Pleurozia purpurea.* High frequency is also shown by *Drosera rotundifolia,* whereas *Scirpus caespitosus* is more patchy in its dispersion. Some of the species more characteristic of hummocks occur rather sparsely, such as *Calluna vulgaris, Potentilla erecta, Rhacomitrium lanuginosum, Cladonia* spp.

An independent estimate of the cover contributed by the several species of the flats by the point method, gave the following result which compares favourably with the estimates incorporated in Table 1.

(Figures = % cover.)

Sphagnum papillosum } S. rubellum	91	Drosera rotundifolia	10
Rhynchospora alba	52	Rhacomitrium lanuginosum	9
Molinia caerulea	43	Eriophorum vaginatum	8
Erica tetralix	34	Pleurozia purpurea	5
Narthecium ossifragum	23	Carex echinata	2
Calluna vulgaris	21	Drosera anglica	2
Eriophorum angustifolium	16	Myrica gale	2
Scirpus caespitosus	11	Polygala serpyllifolia	2
		Carex panicea	1
		Pedicularis sylvestris	1
		Potentilla erecta	1

HUMMOCKS.

One of the most striking features of the bog is the large number of hummocks of *Rhacomitrium lanuginosum* scattered over a more or less continuous carpet of *Sphagnum*. Pure *Sphagnum* hummocks are very infrequent and do not make a significant contribution to the overall vegetation pattern.

The *Rhacomitrium* hummocks are from 10 to over 50 cm. in height and are characteristically rather flat-topped with fairly steep sides. They vary from 40 to 200 cm. in diameter, many of the largest being based on boulders or decaying tree stumps. A longitudinal section of a representative hummock is shown in Fig. 5. The outer shell is composed of a loose layer of living *Rhacomitrium* some 3 cm. in depth. Within this there lies a fairly compact mass of undecomposed organic material consisting mainly of dead *Rhacomitrium* together with a few remnants of *Molinia* and *Eriophorum*. This litter becomes more tightly compacted towards the base of the hummock where it merges into a zone of highly humified peat. The stratigraphy of the peat below this point is similar to that elsewhere in the bog; there is no evidence to suggest that there is any "regeneration cycle".

A total of 28 *Rhacomitrium* hummocks were examined with a view to ascertaining the vegetational succession associated with their formation. The hummocks sampled were those crossed by a series of line transects traversing the bog, at least three being taken from each marked square. Each hummock was divided arbitrarily into three zones, the margin, side and top, which were treated separately when a quantitative assessment of the vegetation was made. The results of these floristic analyses are included in Table 1.

Most of the species present on the flats are to be found on the margins of the hummocks, sometimes reaching their highest frequency there and in some cases extending up the sides. The *Sphagnum* spp. retain their dominance on the hummock margin although *Rhacomitrium* has become more conspicuous. *Erica tetralix, Narthecium, Molinia* and *Eriophorum* spp. are also prominent, while pine seedlings are quite commonly established on the margins of the smaller hummocks. On the sides and top *Rhacomitrium* assumes dominance to the virtual exclusion of the *Sphagnum* spp. Many of the higher plants become less frequent although *Calluna, Molinia* and *Eriophorum* spp. maintain

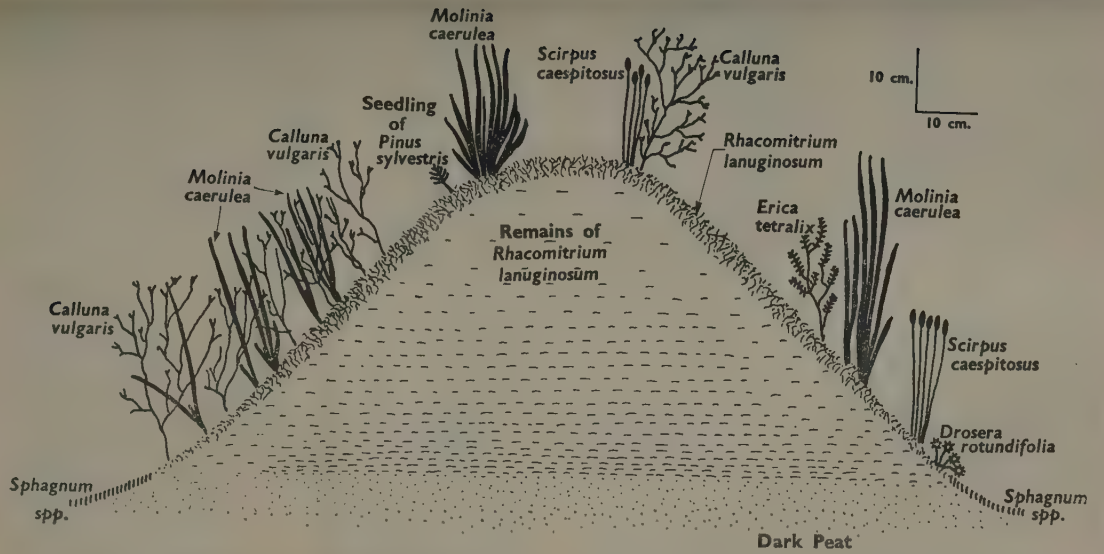
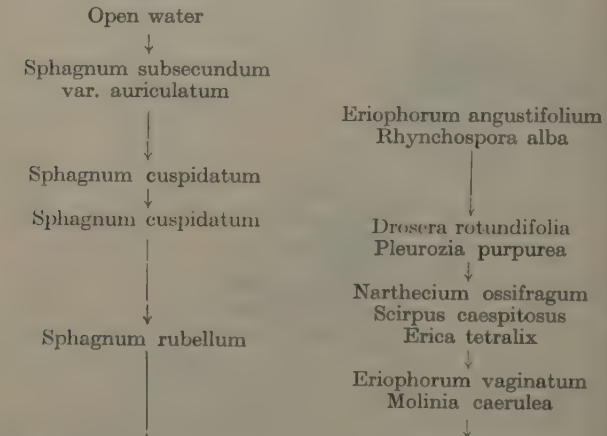


FIG. 5.—Diagram of a longitudinal section of a representative *Rhacomitrium lanuginosum* hummock.

their status. In some cases the domed top of the hummock i bare of all other species, perhaps because, unlike *Sphagnu* hummocks, this part readily dries out. Thus, species such a *Calluna vulgaris, Potentilla erecta,* seedlings of *Pinus sylvestri Hypnum cupressiforme* and lichens, characteristic of the hum mocks, show rather higher frequencies on the margins and/o sides than on the tops. Other species frequently present an showing similar trends are *Erica tetralix,* the two *Eriophoru* species, *Molinia caerulea, Scirpus caespitosus, Narthecium oss fragum, Drosera rotundifolia* (see photo 4).

The vegetation of the hummocks may be considered in term of two parallel plant successions. The mass of the hummock i the product of a succession of mosses acting as builders; thi matrix is at the same time colonised by a series of higher plant their vigour and prominence at any one level or time being function of the height of the evolving hummock above the leve of the ground water table.

Commencing from an open pool, the succession may b represented in this way:—



The *Rhacomitrium* hummocks show no sign of retrogression The evidence, in fact, suggests that each hummock has a distinct

history of its own and builds up to a certain maximum size and there remains, at least for a period, more or less stable. There is no sign of a cycle of build-up and degeneration and it would not appear to be a likely development under the present environmental conditions. Tallis (1958) points out that in the oceanic conditions of west Scotland (as in Ireland) *Rhacomitrium* "becomes overwhelmingly dominant on hummocks which are not actively eroding, at a stage corresponding to the 'Stillstand komplex'." As far as it is possible to judge, this appears to describe accurately the situation in the bog at Kinlochewe.

PINUS SYLVESTRIS.

The distribution of seedlings and small plants of *Pinus sylvestris* was recorded in a series of 17 belt transects, 10 cm. wide, traversing the bog from margin to margin. Dividing the transects according to the portions which crossed the bog surface and those crossing the rim, the following result was obtained:—

	Healthy	*Unhealthy*
Bog surface	1	8
Rim	50	38

There is an apparent association between the occurrence of healthy plants and high cover-value for *Erica tetralix,* suggesting that establishment of pine cannot take place until conditions are at least favourable for vigorous growth of *E. tetralix.* Pine seedlings and small plants are also found on the hummocks in the bog, particularly on the margins of the smaller *Rhacomitrium* hummocks.

Considering both plants of bog surface and rim, age distribution was as follows:—

1- 4 years—67 individuals
5- 9 years—17 individuals
9-30 years— 9 individuals

Growth was extremely slow, 3-year-old seedlings not exceeding 5 cm., while the mortality rate amongst seedlings must be high. Most of those that survive the first 5 years probably persist, but even at ages 15-30 the height is only about 30 cm., one of the tallest measuring 42 cm. There is, therefore, at present no effective colonisation of the bog surface, although plants may become established on the rim.

IV. Measurements of conductivity and acidity of the bog water.

Conductivity.

Water seeps down from the corrie into the bog all along its western perimeter and drains away to the north, east and south. Six inflow and ten outflow channels were identified, but these probably form only the main passages for the entry and exit of water.

Samples from the inflow, outflow and bog waters were collected on the same day in 130 ml. polythene bottles. These were filtered through Whatman No. 1 filter papers and determination of pH (glass electrode) and specific conductivity (Mullard bright platinum cell with bridge and oscillator) made within 48 hrs. The specific conductivity of the water was calculated as reciprocal megohms at 20° C. From this value the conductivity due to hydrogen ions was subtracted to give a final figure, the corrected conductivity or K_{corr}, which provides an estimate of the total electrolytes in solution, apart from hydrogen ions (see Sjörs, 1950a). The results are assembled in Table 2.

Table 2.

Corrected conductivity of inflow, outflow and bog waters.

	No. samples	*Mean Kcorr*	*Standard error*
Inflow channels	6	83	±3
Outflow channels	10	73	±2
Bog pools	8	76	±2
Flats and Sphagnum hummocks	5	84	±8

The concentration of electrolytes in the waters entering the bog is greater than that in the waters draining away, the figure for the bog pools being intermediate in value. A series of 't' tests shows these differences to be statistically significant. Thus, so far as this small sampling is reliable, the inference is that the inflow waters are gently feeding more minerals into the bog than are being carried away in the drainage waters of the outflow channels.

The mean K_{corr} value of 76 for the bog pools is somewhat higher than figures given for similar habitats by other workers (Gorham, 1956a, 1956b; Gorham and Pearsall, 1956). In fact Pearsall (1956) considers that it is unusual for bog water to give a specific conductivity much greater than 50. The value of 76

s consistent with the conclusion that this is not a purely ombrogenous bog.

A notable feature of the data tabulated above is the relatively high K_{corr} value of 84 for water squeezed from the *Sphagnum* of the flats and *Sphagnum* hummocks. The sample is small and the figures show some diversity, having a standard error of ±8; nevertheless the mean is significantly higher than that recorded for bog pools. Results supporting this finding have also been obtained from bogs in other localities. Data, however, are insufficient to interpret this finding as yet, although it may be that the wick-like action of *Sphagnum* shoots, continually presenting a moist surface to the atmosphere, promotes evaporation and thereby some concentration of mineral salts*. In this connection it is noteworthy that water obtained from within *Rhacomitrium* hummocks gave rather lower values for K_{corr} (e.g. 69, 74): the surface of these hummocks readily dries out, restricting evaporation of the moisture within. If certain species of *Sphagnum* do tend to form reservoirs of slightly higher mineral salt concentration this might be a factor contributing to the successful colonisation of *Sphagnum* hummocks by other species; a similar subject for inquiry has been suggested by Goodman and Perkins (1959) in the case of *Eriophorum vaginatum* tussocks. The whole question is worthy of further investigation and may be of considerable ecological importance.

Acidity.

Acidity was measured in the field by inserting the glass electrode directly into the wet peat or, in the case of pools, inflows and outflows, suspending it in open water. The results are given in Table 3.

The first series of results (Nos. 1-7) deals with the main inflow channel. In general, there is a very marked tendency for the pH to fall as the bog is approached. The first value of 5·6 was obtained well outwith the influence of the bog and in the complete absence of *Sphagnum*. The lower regions of the inflow channel (Nos. 2-5) are marked by the presence of *Sphagnum subsecundum* and other species commonly occurring in sites receiving mineral soil water. In the final two readings, taken within the boundary

*Bell (1959) in a reference to the same locality, points to the part played by evaporation in increasing the concentration of electrolytes in bog water.

TABLE 3. MEASUREMENTS OF ACIDITY.

	pH	
Main inflow.		
1.	5·6	*Potamogeton polygonifolius, Eriophorum angustifolium, Juncus kochii.*
2.	5·0	*Sphagnum subsecundum*, Drosera anglica, Eriophorum vaginatum.*
3.	4·7	*Sphagnum subsecundum*, Rhynchospora alba, Potamogeton polygonifolius.*
4.	5·0	*Sphagnum subsecundum** (denser).
5.	4·1	*Rhynchospora alba, Sphagnum subsecundum*.*
6.	3·7	Pool at edge of bog. *Potamogeton polygonifolius, Sphagnum subsecundum*, S. cuspidatum.*
7.	3·8	Adjacent pool. *Eriophorum angustifolium, Sphagnum cuspidatum, S. subsecundum*.*
South end of bog.		
8.	4·2	Pool. Open water.
9.	4·1	Edge of pool. *Sphagnum cuspidatum, S. subsecundum*, Eriophorum angustifolium.*
10.	4·0	Edge of pool. *Sphagnum cuspidatum.*
11.	3·6	Edge of flat. *Sphagnum papillosum, S. cuspidatum, Drosera rotundifolia.*
12.	3·8	Flat. *Sphagnum papillosum, Narthecium ossifragum, Eriophorum vaginatum.*
13.	4·4	Flat. *Rhynchospora alba, Sphagnum papillosum, S. cuspidatum, Molinia caerulea, Carex echinata, Narthecium ossifragum, Drosera rotundifolia.*
14.	3·5	"Island" at centre of pool. *Scirpus caespitosus, Calluna vulgaris, Sphagnum papillosum.*
15.	3·4	"Island" at centre of pool. *Eriophorum vaginatum* tussock.
South end of bog.		
16.	4·5	Pool. *Sphagnum cuspidatum, S. subsecundum*, Eriophorum angustifolium, Juncus kochii.*
17.	4·1	Edge of pool. *Sphagnum cuspidatum, Drosera anglica, Eriophorum vaginatum.*
18.	4·2	Flat. *Sphagnum papillosum, Erica tetralix, Rhacomitrium lanuginosum.*
19.	3·7	Side of hummock. *Rhacomitrium lanuginosum.*
20.	3·8	Top of hummock. *Rhacomitrium lanuginosum.*
Centre of bog.		
21.	4·5	Pool. Floating *Sphagnum cuspidatum.*
22.	4·1	Pool. Sub-aquatic *Sphagnum cuspidatum.*
23.	3·6	Edge of pool. *Sphagnum cuspidatum, Narthecium ossifragum, Erica tetralix, Molinia caerulea.*
24.	3·8	Flat. *Sphagnum papillosum.*
25.	3·2	Flat. *Eriophorum vaginatum* tussock. *Sphagnum papillosum.*
26.	3·7	Base of hummock. *Rhacomitrium lanuginosum, Narthecium ossifragum, Rhynchospora alba, Erica tetralix, Sphagnum rubellum.*
27.	4·0	Side of hummock. *Rhacomitrium lanuginosum, Molinia caerulea.*
28.	3·6	Top of hummock. *Rhacomitrium lanuginosum, Calluna vulgaris* (little).
Outflow at northern end of bog.		
29.	3·8	*Molinia caerulea, Rhynchospora alba, Sphagnum subsecundum*.*

*In all cases, the var. *auriculatum*.

f the bog proper where *Sphagnum cuspidatum* begins to make n important contribution to the vegetation, the pH falls to a evel well below 4.

The second series (Nos. 8-15) was recorded in and around a arge pool at the southern end of the bog. There is a slight liminution in pH from the open water of the pool to the edge, and sharp drop once the flat is reached. The high value of 4·4 (No. 3) is associated with a combination of species (*Rhynchospora, Carex echinata* and *Molinia*) suggestive of a localised area of higher nutrient status. The two final readings, obtained on an "island" of moribund *Sphagnum* at the centre of the pool, are markedly ow as might be expected from the presence of the tussock-forming pecies and *Calluna*.

Sample Nos. 16-20 represent a pool-flat-*Rhacomitrium* ummock sequence at the southern end of the bog. There is a eneral fall in pH, with sharp drops from pool to lawn and from awn to hummock. The fourth series (Nos. 21-28) shows a imilar sequence at the centre of the bog. The drop in pH from ool to flat is again apparent, although in this case values in he hummock do not fall as low as those on the flat.

The final sample (No. 29) is, unfortunately, the only result vailable for an outflow channel. Although the vegetation is in many respects similar to that of the inflow, the pH of the water s distinctly lower, probably as a result of the influence exerted by the bog.

V. Conclusions and summary.

Investigations of certain aspects of the ecology of a small bog n Kinlochewe Forest, Wester Ross, indicate that an earlier description of it as a "raised bog" was inappropriate. The following are the chief findings:—

(a) The bog has originated in a basin of stony and gravelly material.

(b) The peat formed in this basin, nowhere exceeding 120 cm. in depth, itself has a concave surface, the centre lying some 40 cm. below the level of the rim on the E., S., and W.

(c) Some charred material immediately above the underlying mineral basin suggests destruction of a previous vegetation by fire. A swampy birch wood is represented by remains overlying the charred layer. Above this the peat is very

uniform, its composition indicating continuous occupancy o the site by a vegetation essentially similar to that of th present day (i.e. strong representation of *Sphagnum* spp. *Eriophorum angustifolium, Scirpus caespitosus, Molini caerulea*). There is no sign of recurrent series of distinc strata nor lenticular masses of *Sphagnum* such as ar characteristic of "regeneration complex" (Oswald, 1923 Godwin and Conway, 1939). The upper 10 cm. of peat ar darker than the rest; this, together with the abundance o *Calluna vulgaris* and *Rhacomitrium lanuginosum* in th present vegetation may suggest some drying of the surface.

(d) The vegetation consists of a pattern of pools, flats and hum mocks, of which the hummocks contribute the smalles proportion of the total area. Most of them consist largely o *Rhacomitrium lanuginosum*, generally on a basis o *Sphagnum* which has, at least in some cases, built over small prominence (stone, stump). Below, the peat i identical with that elsewhere in the bog. There is no sig of retrogression in the hummocks, nor of any previou generation of hummocks now buried: the vegetation is per haps best interpreted as a 'stillstand komplex'.

(e) Rainfall is by no means the only source of supply of wate to the bog: a number of inflow channels, bringing drainag water from the surrounding hills, are present, while outflo channels release water over a 'lip' in the underlying basin t the N. Conductivity and pH measurements indicate a con tinual gentle mineral "flushing" of the bog.

Grateful acknowledgment is made to Miss U. K. Duncan fo checking the determinations of *Sphagnum* spp.

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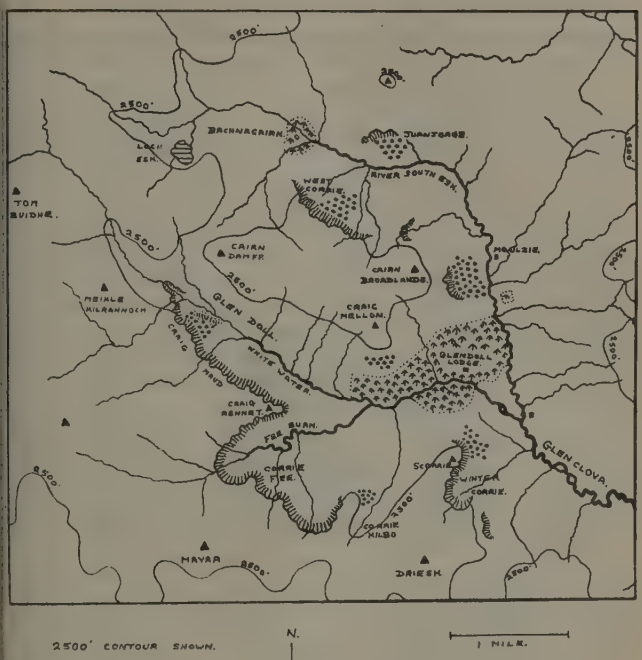
Notes on the Bryophytes of Upper Glen Clova and Glen Doll, Angus (v.c. 90).

Derek A. Robertson and John K. Marshall.

Introduction.

The area covered by this survey consists of two glens at the head of Glen Clova, one of the several glens of northern Angus which run roughly from north to south towards the lowland part of the county, beyond the highland boundary fault. Both glens are roughly 5 miles in length, while the main glen is about 18 miles long. The most easterly fork, down which the River South Esk flows, appears on the Ordnance Survey maps as a continuation of Glen Clova proper, and will be referred to here as Upper Glen Clova. The west pointing fork is called Glen Doll. Some of the high ground situated between these two glens and to the west, was also explored. This, in contrast with the steep-sided glens, is a comparatively gently undulating summit plateau, much of it over 2500 feet above sea level. The whole region (see map, fig. 1) is a representative portion of northern (highland) Angus, and it approaches the border of Aberdeenshire. It is in this region that the summit plateau reaches its maximum elevation. Several of the other Angus glens have their terminations here, and, in many cases besides the two glens which are the subject of this paper, it is here where the valley sides are highest and steepest. Glen Doll is especially forbidding, much of it being bounded by steep cliffs. In addition, the glen sides are gouged here and there by corries, the cliffs of which, like the crags, are the habitat of numerous rare plants, no doubt because of the difficulty of access to grazing animals and humans alike and possibly also because the vegetation, clinging to narrow and unstable ledges, cannot form a stable, closed community. Many of the rarities of this region, first brought to notice by George Don, appear to be plants which cannot withstand competition in a closed community.

A series of excursions was conducted from 1956-59. The vastness of the area and the great difficulty in covering this hilly country necessitated the quick recognition and definition of the principal habitats, and the selection of one representative area, at least, of each of these for intensive collecting. Elsewhere, only superficial collecting was carried out. The species lists, never



IG. 1.—Sketch map of Upper Glen Clova and Glen Doll, adapted from rdnance Survey One Inch Map, sheet No. 50 (revised 1925 and subsequently).

ntended to be exhaustive, apply mainly to the localised areas udied, in order to give a picture of the bryophyte flora of a amed habitat within the area as a whole. For complete lists om Angus, see Gardiner, 1848, Ferguson, 1870, and Fulton, 1912.

HABITATS.

Three major habitats (and major topographical features) were fined within the area, these being, the cultivated valley bottom pplicable primarily to the main glen), the steep valley sides and

the summit plateau. In turn, the valley sides contain other distinct habitats, six in all, the most outstanding of these being the crags and the cliffs of the corries and the steep gullies which seam the valley sides, areas of scree, one of which supports a fair cover of Birchwood, and the sides of streams. This last habitat, while not strictly a habitat of the valley sides, applies only to the portion of the streams where they tumble down into the glens proper from their shallow defiles in the summit plateau, down to where they reach the flatter, alluvial and cultivated floor of the main glen. The best developed bryophyte flora was found at Bachnagairn, where the River South Esk rushes down into Glen Clova from the summit plateau and at which point there is a fairly large piece of woodland almost concealing the deep ravine through which the river tumbles in a series of cascades. Ranking second to this as regards luxuriance is the bryophyte flora of the scree birchwood in Glen Doll. Thus, while the woodlands are really superimposed on basic geological features, they carry very distinctive bryophyte communities, and so they have been considered as special and distinct habitats.

The principal habitats, which in turn will be considered more fully, can be listed as follows:—

1. Cultivated Valley Bottom.
2. Valley sides—
    a. General.
    b. Corries, Crags and Gulleys.
    c. Scree.
    d. Scree with Birchwood.
    e. Streamside with Coniferous woodland.
    f. Streamsides.
3. Summit plateau.

1. *The cultivated valley bottom.* This habitat is found throughout the main glen and also up part of Upper Glen Clova, and in Glen Doll at its confluence with the main glen. The ground is almost perfectly level, the soil is a deep, friable brown earth and across the whole area, the river has cut a winding, pebbly bed with numerous ox-bows. It would appear that this area was once the bed of a glacial or early post-glacial lake extending along much of the upper reaches of the main glen, which has drained away leaving the rich detritus deposited when its waters were still and deep. While no bryophytes of any importance were

noted either in the ploughed fields or in the semi-permanent pastures or on the man-made habitats like walls and footpaths, the sporadic collecting which was carried out did reveal the presence of *Marchantia polymorpha* and *Lunularia cruciata* in the grounds of Glen Doll lodge. Both of these are species which are constantly found near human habitation, the latter almost exclusively so.

2. *Valley sides. a. General.* The valley sides, in contrast with the bottom, are steep and have a thin covering of soil though here and there are deep pockets of heather peat, either alone or overlying gravel. Elsewhere, the underlying rock outcrops, carrying a scanty cover of vegetation, and everywhere there are boulders of varying sizes occurring in greater or lesser concentrations. In spite of the sparsity of soil in this general habitat, there is a fair cover of *Calluna vulgaris* or of *Vaccinium myrtillus*. Everywhere, the valley sides are seamed by shallow defiles marking the courses of streams, some ephemeral, some permanent. In these defiles, the peat has, of course, been eroded away revealing the underlying gravel and boulders, and it has been found that many bryophytes and flowering plants appear to thrive better in this particular situation than elsewhere.

Here and there beneath the cover of *Calluna* and *Vaccinium myrtillus,* or in the shelter of boulders in scree, plants which one commonly associates with woodland occur. These are *Anemone nemorosa, Oxalis acetosella, Digitalis purpurea, Luzula pilosa* and *Blechnum spicant. Luzula sylvatica* also occurs in such situations and, furthermore, extensive patches of that plant occur, quite exposed, around the edge of the summit plateau in places.

All these species are to be found in the remnants of natural woodland still surviving in the glens and it is possible that their presence in the open might indicate that trees once did grow upon the site. On the other hand, as will be explained in more detail later, it is quite possible that their association with woodland while strong in lowland areas, may be weak in upland regions and that they may be flourishing on sites which have never been wooded at any time.

The case of *Luzula sylvatica* is an outstanding one. Typically a woodland plant in lowland regions, it is frequently found in the open on the valley sides in the Glen Clova area in situations which might or might not have been wooded as well as in the small areas

of woodland which remain. On the summit plateau, however, it forms extensive sheets, and although trees did undoubtedly grow there, at least in the more sheltered hollows, there is no evidence of trees ever having grown on the exposed knolls around Driesh and the Scorrie, where this plant is particularly plentiful. It would thus appear that this plant can flourish equally well at all levels from sea level to 2,500 feet and over, but that its association with woodland seems to decline with increasing altitude.

b. *Corries and Gulleys.* Three main corries occur in the area: West Corrie, Winter Corrie, and Corrie Fee, all lying between 1,500 feet and 2,500 feet. Corrie Kilbo, which lies between the last two (see map, fig. 1) is not, strictly speaking, a true corrie since it lacks the precipitous rocky sides of the others and so it has not been considered as such. Because of its remoteness, West Corrie was not studied at all, but Winter Corrie was well worked as was Corrie Fee to a rather lesser extent. Generally speaking, the lower slopes of the corries were more thoroughly worked than their steep walls.

Gulleys form steep shafts up the walls of Corrie Fee and there is a large one ascending the west wall of Winter Corrie. Only the lip and the base of this last gulley were examined. A very noticeable and large gulley in which extensive collecting was carried out ascends the steep eastern face of the Scorrie, forking several times in its upper reaches.

c. *Scree.* Scree areas occur below West Corrie and on the opposite side of Upper Glen Clova at Juanjorge; below Cairn Broadlands (very spectacular), at the foot of the Scorrie, below Craig Mellon, in Corrie Kilbo, below Craig Rennet and below Craig Maud. This latter scree is also very extensive and spectacular and the lower portion, which supports a fair cover of Birchwood, consists of a tumbled mass of huge boulders, some of them as much as 20 feet high.

The first three localities mentioned were scarcely investigated at all, though it was noted that the West Corrie scree and the scree at Juanjorge supported a sprinkling of Birch and Rowan. The Cairn Broadlands scree is still subject to movement in places and some of the few trees there have been badly smashed by these landslides. A little collecting was carried out here and on the Corrie Kilbo and the Craig Rennet screes. On these last two screes, the vegetation is fairly advanced (closed *Calluna-Vaccinium*

stage, as given in Tansley, 1949) whereas at the Scorrie and the Craig Maud screes (the latter above the Birchwood) the vegetation is still in a relatively immature state (late *Rhacomitrium-Cryptogramma* and early *Calluna-Vaccinium* stage, according to Tansley, though actually *Cryptogramma crispa* is scarcely in evidence). It was on these last two screes that really intensive collecting was carried out.

d. *Scree with Birchwood.* Although scattered *Betula verrucosa* and *Sorbus aucuparia* occur on most of the scree slopes, the only true scree Birchwood occurs on the lower slopes of the scree below Craig Maud, at about 1,700 feet. Here, Birches and Rowans of varying ages grow among the boulders and form a reasonably closed canopy in places. Several herbaceous plants characteristic of woodland occur beneath this canopy among which *Anemone nemorosa, Oxalis acetosella, Digitalis purpurea, Luzula sylvatica* and *L. pilosa* feature conspicuously. The comparative inaccessability of this piece of woodland to grazing animals like sheep and deer is indicated by the luxuriant bushes of *Vaccinium myrtillus* topping almost every boulder. Luxurious growths of bryophytes also cover the boulders both deep down among the *Vaccinium* and along the boulder sides.

A very much smaller concentration of Birches was noticed growing among large boulders about 200 yards further up the glen from the Craig Maud Birchwood, at the foot of a steep-sided gulley at the very end of the glen. This concentration of Birches was not explored but might be presumed to be very like the Craig Maud wood.

e. *Streamside with Coniferous wood.* This heading is given to the semi-natural coniferous wood at Bachnagairn, situated at the termination of Upper Glen Clova at an elevation of from 1,500 feet to 2,000 feet. It is just above this wood that the River South Esk leaves the summit plateau, where it occupies a fairly shallow valley, and descends sharply to the bottom of the glen, via Bachnagairn, in a spectacular series of waterfalls. The wood consists mainly of planted *Picea abies* and *Larix decidua*, all about 70 years old. Bachnagairn is the name of an old hunting lodge, the ruins of which can still be seen in the wood. In addition to the planted trees, there are scattered specimens of *Betula verrucosa, Sorbus aucuparia* and *Salix* spp. of varying ages. Seedlings

of conifers occur, but appear not to survive after the first year or so.

Towards the upper limits of the wood, there are a few trees of *Pinus sylvestris* ssp. *scotica*. It is possible that these may be the descendants of the Pines that are known to have occurred in sheltered dips in the summit plateau all around, as is revealed in their stumps and roots protruding from the peat hags. The actual extent of the primeval forest is not known, but it may well have been more or less continuous with the still extensive forests of the slopes of Deeside, about 6 miles to the north. Although the bulk of the conifers at Bachnagairn have been planted, the ground flora has been disturbed very little and the wood is relatively open. It was apparently intended as an amenity and not as a crop.

The gorge through which the stream cascades cuts through the centre of the wood. Its steep, rocky sides support by far the most luxuriant bryophyte communities found anywhere in the area studied, and the vast majority of the bryophytes recorded from Bachnagairn are from this latter habitat. The trees partly conceal the gorge and shield it from direct sunlight, and because of this, several species which demand shading and a high degree of humidity are to be found here and nowhere else in the vicinity.

It must be mentioned in passing that there is another even larger coniferous wood situated at the junction of the two glens. The mature trees of this wood like those at Bachnagairn, are also about 70 years old, and the original plantings were centred around Glen Doll lodge, now a youth hostel. This old wood was again most likely planted as an amenity and the cover is moderately open, but it is now under the management of the Forestry Commission which is establishing close stands of conifers for a timber crop all around and well up Glen Doll itself.

f. *Stream sides.* Areas of coarse or fine shingle at the edges of pools and quieter parts of the streams, and boulders in or bordering their more turbulent stretches are included under this heading. Some bryophytes, like the species of *Fontinalis*, grow characteristically on submerged boulders. The streams lying within the altitudes 900 feet to 1,500 feet are included, and the principal ones are the River South Esk, the White Water and the Fee Burn. The last two were particularly well studied. Below 900 feet, the streams meander across cultivated land, while above

,000 feet, the upper reaches of the streams and the tributaries oining them are in turn fed by numerous flushes seeping out hrough gravel or deep peat towards the edge of the summit lateau.

3. *Summit plateau.* At about 2,500 feet, the steep valley ides level out remarkably to a comparatively gently undulating ummit plateau with scattered undistinguished peaks, many of vhich almost reach or just exceed 3,000 feet. Most of this plateau s blanketed by deep peat, dominated by heather and, here and here, where the peat is shallower, by *Luzula sylvatica* or by ypical plateau plants like *Lycopodium alpinum, Juncus trifidus* nd *Rhacomitrium lanuginosum*, particularly where the ground is gravelly.

There is evidence everywhere of serious erosion of the summit eat. On the Meikle Kilrannoch plateau, two remarkable outcrops of serpentine, each about 100,000 square yards in area, are laid comparatively bare, with deep fissures radiating outwards nto the surrounding eroding deep peat.

On the plateau between Cairn Broadlands and Cairn Damff, too, the peat has been extensively eroded and is traversed everywhere by hollows and deep fissures. In both these areas, up to 5 feet of peat has been eroded away in these peat hags, and in the bottom layers of peat, stumps and roots of Scots Pine, and also of Birch and Rowan are frequently seen, indicating that forest containing Pine, either continuous, or more likely scattered, was once established on the summit plateau.

The deep peat of the summit plateau is most unproductive bryophytically, but towards the edges of the plateau where the ground begins to fall away sharply, and where the peat thins out, numerous flushes are found. These high plateau flushes, in contrast with the peat, support a rich and luxuriant bryophyte flora. The regions where bryophyte flushes have been most intensively studied are in the Scorrie—Driesh-Mayar-head of Fee area (including the rim of Winter Corrie and Corrie Fee), all at about 2,500 feet; the Meikle Kilrannoch plateau (over 2,750 feet) and the Craig Mellon-Cairn Damff-Cairn Broadlands plateau (over 2,500 feet).

In addition to the poor bryophyte flora of the deep peat and the rich bryophyte flora of the flushes, certain species were also found on areas of gravel and boulders not blanketed by peat, as

at the summit of Cairn Broadlands (though the serpentine outcrops appear to be too unstable to support the growth of bryophytes), and four moss species were also found on deer droppings on the summit plateau.

NOTES ON SPECIES LISTS.

A total of 77 Hepatics and 128 Mosses was listed from the various habitats investigated in the upper Glen Clova and Glen Doll areas. By no means can this be regarded as a complete total indeed, the lists given by Gardiner (1848), Fergusson (1870) and Fulton (1912) would indicate that about 65 more mosses could be added to this total, these having been found at one time or another in the area studied. The emphasis of the collecting expeditions was to shed further light upon the general ecology of the bryophytes of this region, and not to compile exhaustive lists of species or to look for rarities not recorded by previous investigators. Nevertheless, in comparison with the existing lists, the number of hepatics recorded from the Glen Clova area has been considerably increased, and in the case of several bryophytes what were single records from other parts of Angus have been further substantiated as a result of these investigations.

The bryophyte nomenclature follows that of the Annotated list of Hepatics (Jones, 1958) and the Annotated list of Mosses (Richards and Wallace, 1950).

The writers would like to express their gratitude to Miss U. K. Duncan and to Mr. E. C. Wallace for so kindly checking the identification of the more critical species. Miss Duncan also read through the script and her helpful criticism and advice were greatly appreciated.

The authors are also indebted to the heads of the departments of Botany, Zoology and Geology in the University of St. Andrews for the use of the Glen Doll field station during the times when these investigations were carried out.

The species have been listed, and the numbers following them (1 to 8) indicate the habitats where they were found.

1. Valley Bottom. (Fields, paths and field walls near Braedownie).
2. Valley sides. (General).—Below Winter Corrie and Glen Doll.
3. ,, ,, (Corries and Gulleys).—Winter Corrie, Corrie Fee, Scorrie.
4. ,, ,, (Scree). Craig Maud and below the Scorrie.

„ „ (Scree with Birchwood).—Below Craig Maud.
„ „ (Stream-side with Coniferous wood).—Bachnagairn.
„ „ (Stream-sides).—Fee Burn, White Water, River South Esk.
Summit Plateau. (Driesh, Meikle Kilrannoch and Cairn Broadlands).

LIST OF HEPATICS.

Conocephalum conicum	3 4 5 6
Lunularia cruciata	1
Preissia quadrata	3 7
Marchantia polymorpha var. polymorpha	1
Riccardia multifida	6
R. latifrons	6
R. pinguis	1 2 3 7
Pellia epiphylla	2 7
P. neesiana	3
Metzgeria furcata var. furcata	5 6
M. pubescens	3
Blasia pusilla	3 7
Anthelia julacea	8
Ptilidium ciliare	2 3 4 5
P. pulcherrimum	5 6
Blepharostoma trichophyllum	8
Bazzania trilobata	2 3 4
B. tricrenata	3 4
Lepidozia reptans	5 6
L. trichoclados	5
Calypogeia trichomanis	2 5 6
C. fissa	5
Lophozia ventricosa var. ventricosa	2 5 6
L. ventricosa var. longiflora	6
L. porphyroleuca var. porphyroleuca	6
L. alpestris var. alpestris	3 5 6
L. incisa	2 3 8
Barbilophozia floerkei	3 5
B. atlantica	3 4
B. attenuata	4 6
B. quadriloba	5
B. lycopodioides	8
B. barbata	4
Tritomaria quinquedentata	2 6
Chandonanthus setiformis var. setiformis	2 4
C. setiformis var. nemoides	3
Sphenolobus minutus	3
S. saxicolus	3 5
Anastrophyllum donianum	6

Anastrepta orcadensis	2 3 4 5
Gymnocolea inflata var. inflata	7
Solenostoma triste	3 6 7
S. pumilum	7
S. cordifolium	2 3 7
S. sphaerocarpum	8
Plectocolea obovata	6
P. hyalina	6
Nardia compressa	6
N. scalaris	3 6 7
Jamesoniella carringtonii	4
Marsupella emarginata	6
M. aquatica var. aquatica	7 8
M. aquatica var. pearsonii	6 7
Gymnomitrion concinnatum	7
Gymnomitrion obtusum	3 4
Mylia taylori	2 3 4 5 6
Plagiochila asplenioides var. asplenioides	2 5 6 7
P. asplenioides var. major	5 6
Lophocolea bidentata	1 3
L. cuspidata	5 6
Chiloscyphus polyanthos var. rivularis	7
Cephaloziella starkei var. starkei	3
Cephalozia bicuspidata var. bicuspidata	6
C. connivens	5
C. media	5
Cladopodiella fluitans	7
Nowellia curvifolia	6
Douinia ovata	5
Diplophyllum albicans	2 3 5 6
Scapania umbrosa	5 6
S. gracilis	8
S. nemorosa var. nemorosa	7 8
S. nemorosa var. alata	7 8
S. degenii	8
S. undulata var. undulata	6 7
S. undulata var. dentata	6
S. uliginosa	8
S. paludosa var. paludosa	8
S. compacta	3
Radula complanata	3 5 6
R. lindbergiana	3
Lejeunia patens	6
Frullania tamarisci var. tamarisci	2 4 5 6

LIST OF MOSSES.

Sphagnum palustre	2 6
S. magellanicum	7
S. papillosum	2 6
S. subsecundum	6

S. fimbriatum	6
S. fuscum	7
S. rubellum	2 7 8
Andreaea alpina	2 4
A. rothii	4
Atrichum undulatum	1 2 6
Polytrichum aloides	2
P. alpinum	3
P. piliferum	1 2
P. juniperinum	2 5 6
P. formosum	6
P. commune	1 2 6
Fissidens bryoides	2
F. osmundoides	2 3
F. adianthoides	2
Distichium capillaceum	2 3 5 6
Ceratodon purpureus	1 2
Blindia acuta	7 8
Dicranella squarrosa	2 7
D. rufescens	2 7
D. subulata	2
D. heteromalla	1
Dichodontium pellucidum	2 6 7
Dicranoweissia cirrata	1
D. crispula	1 4
Dicranum falcatum	6 7
D. blyttii	2
D. starkei	2
D. scottianum	2
D. fuscescens	2 6
D. majus	2 3 5 6
D. bonjeani	7
D. scoparium	1 2 3 5 6
Dicranodontium uncinatum	2
Campylopus piriformis	2
C. flexuosus	2
C. atrovirens	2 7
Leucobryum glaucum	2 8
Encalypta vulgaris	1
Tortula muralis	1
Cinclidotus fontinaloides	7
Barbula hornschuchiana	7
B. rigidula	7
B. spadicea	7
B. recurvirostris	7
Trichostomum tenuirostre	2
Grimmia apocarpa	2 4
G. alpicola	4
G. pulvinata	1 2
G. torquata	2 4

G. patens	2 3
Rhacomitrium aquaticum	3 7
R. fasciculare	3 4
R. heterostichum	3 4
R. canescens	2 4 7
R. lanuginosum	2 3 4 8
Funaria hygrometrica	1
Physcomitrium pyriforme	1
Tetraplodon mnioides	8
T. angustatus	8
Splachnum ovatum	8
S. ampullaceum	8
Tetraphis pellucida	5 6
Pohlia nutans	1 2
Plagiobryum zierii	2
Anomobryum filiforme	2
Bryum warneum	2 7
B. pallens	2 6 7 8
B. pseudotriquetrum	7
B. argenteum	1
B. alpinum	2 3 7
B. alpinum var. viride	7
B. capillare	1
Mnium hornum	2 3 4 5 6
M. longirostrum	6
M. undulatum	3 4 5 6
M. punctatum	6 7
Aulacomnium palustre	2
Bartramia halleriana	2
B. pomiformis	2 3 4
B. ithyphylla	3 4
Philonotis fontana	2 7 8
Breutelia chrysocoma	7
Ptychomitrium polyphyllum	2 3 5 6
Zygodon viridissimus	2
Orthotrichum rupestre	2 3
Ulota crispa	5 6
Fontinalis antipyretica	7
F. squamosa	7
Climacium dendroides	1
Antitrichia curtipendula	5
Neckera crispa	3
Hookeria lucens	2 5 6
Thamnium alopecurum	6
Thuidium tamariscinum	5 6
Cratoneuron commutatum	7
Campylium protensum	7
Drepanocladus revolvens	7
D. uncinatus	6
Hygrohypnum ochraceum	2

H. eugyrium	2
Acrocladium sarmentosum	7
A. cuspidatum	1
Isothecium myurum	5
I. myosuroides	5 6
Camptothecium sericeum	1
Brachythecium rivulare	6 7
B. rutabulum	1
Eurhynchium praelongum	2 5 6
E. riparioides	6 7
Orthothecium rufescens	3
Pseudoscleropodium purum	1 2
Pleurozium schreberi	2 5 6 8
Plagiothecium denticulatum	5 6
P. silvaticum	6
P. undulatum	2 5 6
Hypnum cupressiforme	2 3 5 6 8
H. cupressiforme var. filiforme	5 6 7
H. cupressiforme var. ericetorum	4 8
H. hamulosum	2
Ptilium crista-castrensis	3 5 6
Ctenidium molluscum	5 6
Hyocomium flagellare	6
Rhytidiadelphus loreus	2 3 5 6
R. triquetrus	2 5 6
R. squarrosus	1
Hylocomium splendens	1 2 3 5 6 7 8

REMARKS.

Habitat No.	1	2	3	4	5	6	7	8
No. of Hepatics	4	15	28	13	25	33	18	11
No. of Mosses	22	62	23	14	25	42	35	14
Total	26	77	51	27	50	75	53	25

A total of 26 Bryophytes was recorded from the cultivated lley bottom, 27 were recorded from the scree areas and 25 were corded from the summit plateau. These were the lowest figures om the eight habitats considered, and the paucity in the first se is undoubtedly due to cultivation and other human inter- rence. In the case of the scree areas, the scarcity of soil and the nerally unstable nature of the habitat might account for a low ryophyte total, while the scarcity of species on the summit ateau may be due to the general uniformity of the habitat, the most universal presence of deep peat, and possibly to altitude.

At the other extreme, the highest totals of Bryophytes have en recorded from the valley side habitat and from the stream de with coniferous woodland at Bachnagairn, 77 species being

recorded from the former and 75 from the latter. A more careful consideration of the various habitats leads one to suggest that the total for the valley sides is highest only because it is the most widely spread habitat and because it is a much more composite habitat than any of the others. However, the writers have considered that to sub-divide that habitat further might also call for the sub-division of certain other stated habitats already of limited area, and this in turn would obscure their individual recognition and definition.

Bearing these facts in mind, it would seem that Bachnagairn a well defined habitat of limited area could be regarded as carrying the richest bryophyte flora as regards numbers. Further, the shaded, humid conditions of this wooded gorge seem to favour the maximum growth of all species present, and the spreading carpets of mainly pleurocarpous mosses are a feature more conspicuous here than anywhere else.

As regards totals of mosses, similar remarks can be made. Thus the cultivated valley bottom, the screes and the summit plateau yield the smallest number of species, and the valley sides and Bachnagairn have yielded the largest numbers of species.

In the case of the Hepatics, however, it seems that while the smallest numbers are recorded from the cultivated valley bottom, the screes and the summit plateau habitats, as for the Mosses, the valley sides do not seem to be as rich in species as the corries, 28 species having been recorded from that habitat compared with 15 from the valley sides. The highest species total (33) was recorded from Bachnagairn.

Apart from these findings, based on totals, it has been found that certain species have an association which varies from weak to strong, with certain habitats. Particular attention was paid to obviously woodland and less obviously woodland species to see if these would throw further light on the true status of so-called relict woodland vegetation generally.

Species such as *Mnium hornum*, *Hypnum cupressiforme*, *Hylocomium splendens* and *Dicranum scoparium* occur in the wooded areas of the glens, also outside the woods, in a variety of other habitats; anywhere, it would appear, where there is a sufficient accumulation of soil and sufficient shelter. Their association with woodland, therefore, seems to be a weak one, yet these species have been found to be associated with plants that one is tempted

o regard as truly woodland species, like *Anemone nemorosa* and *Oxalis acetosella* either under Heather on the valley sides or in the helter of boulders in stable scree.

It seems feasible to presume that these flowering plants, like he mosses mentioned, are only weakly associated with woodland, t least in upland areas (they have been noted growing in open situations in other upland areas in Britain, as far south as upper Teesdale). In lowland regions, the association of these flowering plants with woodland would appear to be most definite, though t must not be forgotten that cultivation and other human interference may have exterminated them from habitats other than woodland where they may once have survived. Likewise, the association of *Mnium hornum* with woodland is more positive in owland areas of Britain. In the glens studied, and possibly in upland areas generally, it might be that the ecological requirements of many plants which are definitely woodland species in owland areas, are here met with in areas not covered by trees and which may never have been covered by trees.

These considerations, in the estimation of the authors, must be borne in mind when considering whether familiar woodland species of plants found growing on the open hillside are actually the relict ground flora of a vanished woodland.

A strongly positive association with woodland is found in species such as *Ptilidium pulcherrimum, Radula complanata, Nowellia curvifolia, Lepidozia reptans, Scapania umbrosa, Plagiochila asplenioides* var. *major, Ulota crispa, Tetraphis pellucida, Isothecium myosuroides* and *Antitrichia curtipendula.* This strongly positive association is because so many of these species occur almost exclusively on the bark of trees, living or dead. Therefore, they would hardly be of use as indicators of a now vanished woodland as presumably there would be other obvious signs such as half buried logs or branches associated with these species should they be found in the open.

Of all the truly woodland bryophytes just mentioned, only *Plagiochila asplenioides* var. *major* seems to grow regularly on woodland soils and it may, therefore, seem feasible to suggest that this species at least could be regarded as a true relict woodland species should it be found on open ground with no other signs of the now vanished trees. However, no plants were ever noticed growing in the open, and it may well be that the more positive

the association of a plant, angiosperm or bryophyte or otherwise, with woodland, and correspondingly the greater its reliability as an indicator of woodland, the sooner the plant in question perishes once that woodland is cleared.

This possibility is further supported by the fact that *Plagiochila asplenioides* var. *major* was observed frequently in the 70-year-old wood around Glen Doll Lodge. This wood did once extend to cover a considerable area on the south bank of the White Water, but this latter part was felled during World War II (in 1943), and a recent examination of the site has revealed no trace of *Plagiochila asplenioides* var. *major* (after a lapse of 15 years), though one would feel certain that it did occur before the trees were felled.

Finally, the discovery of *Radula complanata* growing on boulders at over 2,000 feet at the edge of Corrie Kilbo throws further doubt on the true status of "relict woodland plants". This species is commonly associated with the bark of living trees at lower elevations, but it would appear that it regularly adapts itself to a saxicolous habitat at 2,000 feet and over, spreading over boulders like the allied *R. lindbergiana*, a species found commonly at this altitude.

As with the other "relict woodland species", and particularly *Luzula sylvatica* referred to earlier, the occurrence of *Radula complanata* on boulders at 2,000 feet is an example of a species commonly regarded as a woodland plant, flourishing in a non-woodland habitat simply because its ecological requirements are satisfied in an open, upland terrain, at a considerable greater elevation than that most characteristic of it. Again, association with trees diminishes with increasing altitude.

SUMMARY.

A series of expeditions to the upper reaches of Glen Clova and Glen Doll and the neighbourhood was undertaken in the summers of 1956-59. Eight distinct habitats were recognised and bryophyte collecting in representative areas of each of these habitats was carried out.

A total of 77 Hepatics and 128 Mosses was obtained. The lists of Mosses obtained previously by Gardiner (1848), Fergusson (1870) and Fulton (1912) indicate that a great many species have been overlooked, but the aim of these expeditions was mainly to

shed light on the ecology of the bryophytes of this region rather than to compile exhaustive species lists.

Particular attention was paid to species which have an association, ranging from weak to strong, with woodland, in an attempt to provide further evidence regarding the true nature of "relict woodland species". It would appear that the species most strongly associated with woodland, and potentially the most reliable relicts, disappear soon after a wood is felled.

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A Note on the Cytology of some Scottish Mosses.

Margaret I. Wilson and J. H. Burnett.

In 1957-58 one of us commenced an examination of the cytology of Scottish mosses but, as there now seems little chance of continuing this work, the facts are presented here.

In most cases meiosis was examined in spore mother cells (S.M.C.) squeezed from capsules in the manner of Lewis (1957) although in some species it was also necessary to scrape S.M.C. from the extruded columella to which they adhered, e.g., *Tortula muralis*. S.M.C. were either fixed for fifteen minutes in Carnoy-Le Brun (equal parts by volume of absolute alcohol, glacial acetic acid and chloroform), or macerated immediately in a drop of N. HCl, warmed and the superfluous fluid drained off. In either case the S.M.C. were then mounted in a drop of acetic-orcein and squashed or smeared. Pre-mordant fixatives to improve staining were not necessary with our material but the acid maceration cleared the cytoplasm of oil globules and other refractive granules which interfered with observation. Successful permanent mounts were made by a modification of Conger and Fairchild's quick-freeze method (1953), ordinary ice being substituted for dry ice.

Table 1 lists the species, their localities and periods when material was collected.

Table 1.

Species, localities and dates of collection.

Ceratodon purpureus	Wall, Hurley Hawken, Perthshire	November, 1957
Barbula unguiculata	Wall, Hurley Hawken, Perthshire	November, 1958
Tortula muralis	University Botanic Garden, rockery, St. Andrews	March-April, 1958
	Concrete anti-invasion blocks, West Sands, St. Andrews	
Funaria hygrometrica	Pots in greenhouse and cold frames, University Botanic Garden, St Andrews	March-April, 1958
Brachythecium rutabulum	University Botanic Garden, St. Andrews	March-April, 1958

Ceratodon purpureus (Hedw.) Brid.

The chromosome number was $n = 13$ and the large bivalent detected by Steere et al. (1954) and Varaama (1956) was obvious.

This haploid number has now been recorded from Japan, N. America, Europe, England and Wales (Wylie, 1957). However, in our material there was considerable "stickiness" in prophase stages and numerous irregularities including inversion bridges and fragments in later stages of meiosis. Such irregularities have not been recorded before in this species but it is not clear whether they were due to inherent cytogenetical causes or to a natural "cold shock", for the material was collected during extremely cold weather.

Barbula unguiculata Hedw.

Our material had the same haploid number, $n=13$, found in German and Finnish material (Jachimsky 1935: Varaama 1950) and the chromosome complement appeared to be similar with the occurrence of a large symmetrical bivalent.

Tortula muralis Hedw.

Carnoy-Le Brun fixation was essential for this species where there were numerous, small chromosomes. Chromosome numbers previously recorded together with those found by us are shown in Table 2.

TABLE 2.
CHROMOSOME NUMBERS RECORDED FOR *Tortula muralis*.

umber	*Locality*	*Notes*	*Reference*
± 2	St. Andrews, Scotland	Typical plants	Wilson & Burnett
± 2	St. Andrews, Scotland	Typical plants	Wilson & Burnett
– 30	? Surrey, England	Claimed to be a hybrid derivative	Woods in Vaarama, 1956
	St. Andrews, Scotland	Typical plants, exposed site	Wilson & Burnett
– 45			
± 2	Bayfordbury, England	var. *rupestris*	Vaarama, 1956
	Stamford, California	—	Steere, *et al.*, 1954
	? Surrey, England	—	Woods in Vaarama, 1956
± 2	Bayfordbury, Hertford, England	—	Vaarama, 1956
±	Island Mahee, Co. Down, Ireland	—	Vaarama, 1956
	Berkeley City, California	Typical plant	
	Botanic Garden, Berkeley, California	Similar to f. incana (Br. & Sch.) Mörken	Vaarama, 1953

It will be seen that there is a wide range from 23-66 and that, allowing for uncertainties in counting, the basic number could be

related to x = 5, 6, 12 or 13, all of which have been suggested previously (Steere, *et al.*, 1954; Varaama, 1953, 1956; Wylie, 1957). Wylie's suggestion of x = 12 or 13 is based on the chromosome numbers in the genus as a whole.

Morphological diversity is characteristic of this species and there are numerous described forms, but none are sufficiently distinct to enable a clear and useful taxonomic separation to be made (Steere, 1939). The cytology of the species shows a similar degree of variation and it will be necessary to undertake an experimental taxonomic investigation on a wide range of samples before the species can be understood. Meanwhile, there is an obvious superficial similarity between the situation in this moss and a polyploid, amphi-apomictic, angiosperm complex such as *Poa pratensis*. In our material we could not correlate any distinguishing morphological or ecological features with chromosome number nor was there any indication that the $n = 28 \pm 2$ material was of hybrid origin (cf. Woods in Varaama, 1956).

Funaria hygrometrica Hedw.

Our material was remarkable for its poor spore production. Only a few mature capsules were well filled with spores, and the spore size was very variable. The majority of capsules were either empty or contained only a few tens of spores and S.M.C. were equally elusive. Only one countable polar view was obtained and this gave $n = 14$. While this agrees with the count for the "greenhouse" race of California we have found no reference to low spore production, such as we encountered, by any previous investigators of the cytology (Wettstein, 1924; Varaama, 1950, 1953, 1955; Steere, *et al.*, 1954).

Brachythecium rutabulum (Hedw.) B. & S.

Both meiotic and mitotic chromosomes have been examined in this species. Our material was all $n = 12$ which differs from Sinoir's $n = 11$ (1952) or Holmen's $n = 5$ and 10 (1958) on Danish material. Inversion bridges occurred in both meiotic divisions in our material and they were also observed by Holmen in his tetraploid material. Lagging chromosomes were also common in our material. This suggests that the basic number is x = 5 or 6 and that higher numbers have been derived through autopolyploidy.

Our observations have extended the knowledge of moss chromosome numbers to Scottish material and, in the case of *Brachythecium rutabulum* and *Tortula muralis,* provided new counts for the species. They also raise the interesting problem of the nature of polyploidy in mosses. On the whole there is a tendency to attribute polyploidy in natural populations of Spermaphyta and Pteridophyta to the consequences of hybridisation followed by chromosome doubling, i.e. allopolyploidy. In the mosses it is possible that simple chromosome doubling, i.e. autopolyploidy, plays a more important rôle. Our observations on *Ceratodon purpureus* suggests that the chromosomes of some mosses may be quite susceptible to natural "cold shock" and Mrs. Woods has told us that similar effects may be induced in species of *Tortula* when placed in a refrigerator. Moreover, the kinds of cytological aberration noted here and by Holmen (1958) are often held to be characteristic of autopolyploid plants. Autopolyploidy could arise in mosses through "cold shock" leading to the formation of restitution nuclei of higher ploidy or through regeneration, with chromosome doubling after mechanical damage. If these are the principal mechanisms causing polyploidy in mosses, the phenomenon would be of a different character from that in higher plants and, indeed, it would reflect the fact that the group is less effectively buffered against environmental disturbance. It is clear that an investigation of the nature of polyploidy in mosses is most desirable.

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Modern Botanical Thought: Palaeobotany*.

By T. M. Harris.

What Palaeobotany is and what it tries to be are quite different things. It wishes it were the whole of Botany, repeated many times for past periods. It would thus be as diverse as Botany is, but multiplied. In fact, it has a unity imposed by its awkward and limited material and it is still true that its main achievements can be described in a single moderate sized volume.

In this lecture I shall divide palaeobotany, but only to make my points clearly. My divisions are artificial and most of the best researches cover several and I am sure quite different divisions could be made just as well.

Palaeobotany—or as I prefer to call it—fossil botany, shall first be divided then into Pure and Applied fossil botany. The one object of a pure fossil botanist in studying a fossil is to know about an ancient plant; he wants nothing further. The applied fossil botanist studies his fossil in order to get facts which he will apply to another branch of science, though this may be itself the purest science. I will divide applied fossil botany according to the nature of the application. Three important ones I shall describe are Geographical, Geological and Botanical, which I shall take in that order. But first I shall say something about pure fossil botany and I will end with pure fossil botany.

The pure fossil botanist tries his hardest to be an ordinary botanist. Let us think what an ordinary botanist would do if you gave him, say, a new kind of fern and told him to learn all he could and then to publish. He demands unlimited live plants: at least I hope he does. Perhaps after a year or two he produces a sumptuous memoir on its form and structure and then he begins on more intimate things, its genetics, physiology and the rest. It is hardly fair to say that this would keep him working for numberless lifetimes because most of these are doubtless common to all plants; but if we limit ourselves to what is rather special to this plant, for example to the physiology causing it to develop its visible form, it is clear he would be long occupied.

*Being the substance of an address to the Society delivered on 19th November 1959.

Now take a fossil botanist and give him the same fern as a fossil. We do not give him unlimited live specimens, oh no! we give him just ten leaf fragments and no more, and not even well fixed and preserved but altered to a thin film of coal. He gets to work and in a day or two perhaps he is ready to write about everything he has learnt. When he does in fact start, writing will depend on his skill and vigour, and, of course, his luck with the material. If he is rather supine he writes straight away, and his paper may be little more than the descriptions of his photographs. Often enough that is all that the material and his technique allows, but he should at least wish ardently to go further and overcome the badness of the material. I have heard my former teacher, Hamshaw Thomas, say be believed that a compressed fossil plant still retained every original cell, and if we fail to see all these cells, then that is our failure. Well, we do not yet know how to see all these cells, but with hard work and good luck with the specimen we can often see a large number.

I will give a modest example of the way our fossil botanist with the fossil fern can overcome his difficulties and go further. Above most things he will want to study its sorus and sporangia; they will be concealed in the rock and the back of the leaf will be exposed. This is because the sporangia make the under side rough and the rock splits along the smooth side.

A good many years ago, at a time hardly to be called modern, Professor Walton devised his balsam transfer method for turning a compressed fossil over. It is a good method (apart from the fact that it is the only one we have) for it only takes half an hour and very little skill. But think for a moment of the botanist with the living fern; when he wants to see the back he turns it over and never even thinks himself lucky.

Then another way in which he can act is to look for things which the botanist can afford to neglect for the very good reason that he can do what he wants without them. That is why the fossil botanist labours with the plant cuticle. Take, for instance, a conifer. Fossil conifer twigs are common, but most of them show rather little and they look so much alike that you may often be unsure when you have a dozen specimens how many species you have. Still less are you sure, when you try to identify them with the specimens described by others. If you diagnose them as a new species you may run out of facts in five lines.

But prepare their cuticles and you see lots of character, and your diagnosis will occupy a whole printed page. You will easily make up your mind whether your specimens are identical with one another and then with those of another man, provided he has figured his cuticles well. Again compare the fossil botanist with the man who walks into a grove of a new kind of Conifer. He considers whole trees showing dozens of characters; he could write a diagnosis of several pages if he wanted without going beyond a hand lens; he is not troubled by doubt whether two twigs with different leaf forms are the same species, he can see they are on the same branch. Nor will the problem of whether one tree and the next is the same species delay him. Why should he bother with the leaf cuticle, or indeed any character finer than necessary? Curiously enough morphology has now learnt from the fossil botanist that the cuticle may provide facts worth while to him, but this was unexpected.

It has taken fossil botanists an unconscionable time to learn to look at such things. As far as I know, the first fossil cuticle was prepared and figured in 1834, though figured badly and carelessly interpreted. Some good work was done on cuticles in 1867, but only as an incidental curiosity and not until after 1900 did anyone study them with purpose. Perhaps a reason is that fossils are often so preserved that cuticles have perished, perhaps a reason is that people told one another that since the cuticle was the outermost part of a plant it was most subject to the influence of the environment and thus as wayward as the weather, while the xylem core was the plant's heart, true and constant. I suspect these are not reasons but excuses and the reason is that the cuticle adds considerably to your work and if you study it properly you will quarter your output of new species. I have laboured the cuticle because it illustrates a respect in which fossil botany has grown up. Pure fossil botany is the child of pure plant morphology and at first it took its ideas straight and unquestioned from its mother. In many respects it still remains a little child, its hand firmly in mother's and taken willy-nilly and, indeed, without questioning the way mother decides to go. But in this small matter it goes alone, even if a little timidly and sometimes scolded for waywardness. It is quite time, too, now that mother has gone after sporogenesis and embryo sacs and along paths unsuited to her child's footsteps.

But is this sort of thing worthy to be called "thought"? It is not much more than using good sense to get round practical difficulties. Should we call Professor Walton's research on the deformation of plants under compression thought? I think I would, though again it is closely related to practical research problems. What I am sure is "thought", in the sense of this lecture, is what I fancy only rarely and briefly enters the pure fossil botanist's head, and that is, why in the world is he working so hard? It is on this I shall end my lecture.

Now I turn to my applications, and I mentioned three. The Geographical application is the use of knowledge from fossil plants to learn and understand plant distribution in the ancient world and the climates at those times, the two being closely related. Its aim, too, is to understand present plant distribution.

The Geological application is to determine the age of rocks and consequently overlaps the Geographical application.

The Botanical application is to use knowledge from fossil plants to solve problems of comparative morphology and evolutionary history and to give the basis for natural classification.

I turn to the first of my applications, the Geographical, and I shall select as an example the research of Professor Szafer on the Upper Tertiary, Pliocene flora of Kroscienko in Poland. This is a large flora, chiefly consisting of seeds preserved in the soft clay of a brick pit, and although the papers are in Polish he gives an English summary of 70 pages.

Szafer began in the ordinary way by comparing his seeds with recent ones and decided that over half are more or less securely identifiable with living species. He then faced the usual problem which everyone working on Tertiary plants faces, the problem of deciding both the age and the climate. The two are inseparable as it seems that in the Tertiary there was a very slow progressive cooling and with it migration of plants southwards. Since it is his special interest, he develops this application of plant migration most vigorously. As you will readily see, once he has a firm identification, Szafer ceases to be the pure fossil botanist and applies his identification to his main interest. Here he has altogether too much freedom of choice for his peace of mind. He must indeed proceed by comparison with other ancient floras and with living floras, but he can treat his facts as he wishes and his conclusions must depend very largely on his treatment. With

a large number of facts of uncertain weight the possibilities are endless. However, he puts forward a positive hypothesis as the best he can and invites attack cheerfully. Having no independent evidence of age, he decides in favour of Mrs. Clement Reids' outlook and analysis. She favoured comparison of whole floras rather than selected important species, but he goes beyond Mrs. Reid in detail and defines vegetational units more narrowly in a way which gives him more results, but also adds greatly to the bulk of data he must handle. Of course, too, he has the advantage that additional facts have been learnt since her time. It is the great bulk of diverse data that he handles, successfully as it seems to me, that I find impressive. I will mention some of his conclusions, not all put forward with equal assurance.

His flora is Pliocene, and already by the Pliocene the European flora was diverse. South of the great mountain mass of the Alps and Carpathians there was, in the Pliocene, a flora little different from that of the previous period, the Miocene; but to the north (and this includes Szafer's flora) a drastic change had occurred and a largely new flora had appeared. The nearest we know to the Miocene flora and to the Pliocene flora, south of the mountains is what now grows in S.E. United States, along the Atlantic coasts; but in the northern Pliocene this was succeeded by a flora more like that of Central Japan and certain parts of China. In time this, too, was diminished and exterminated by a cooler climate and then by the glaciation of the Pleistocene. There was in addition to these another flora in the Pliocene, a flora of the mountains of which we have already some knowledge. Szafer finds it easier to think of the new floras of successively colder phases descending a few thousand feet down the mountains than a few thousand miles from the far north. His comparisons suggest a much more oceanic climate and one which avoids the bitter cold of the present Polish winter. Summer would be only a little warmer, but the average temperature would be as much as 10° C. higher, and moreover the plants were spared serious drought.

One final remark on the Geographical application. As I have said, the problem of past temperature is entangled with the problem of age and the one set of determinations is used to tell both. Plants have indeed been called "the thermometers of the Ages". Now temperature is physical, and physical measurements are best made with physical instruments, and ancient plants of

somewhat uncertain nature seem poor instruments, though possibly the best we have. I am thus glad that my colleagues tell me that it has become possible to determine the mean temperature of the sea in which a limestone was deposited by purely physical measurements. When Szafer can know from other evidence what the mean temperature was in the Polish Miocene, he may be able to use his Botanical facts to go further and more securely.

Geologists use fossil plants in the same way as they use fossils generally, to determine the age of rocks. I need say nothing about the way they make their comparisons; the principles are familiar and I do not think there has been much change in the way fossil plants have been used for this purpose for a long time—refinements and improvement yes, but not a change in outlook. There has, however, been one strictly modern development, the use of spores and pollen dispersed through the rocks, as zone fossils. They have several great advantages over ordinary fossil plants. They are much commoner and easier to collect, a gram of shale may yield all you want. Then the way of extracting and mounting the spores can be followed like a cookery recipe and it is not even necessary to do it yourself for technicians can be trained to do it very well. It is even said that technicians can do all the microscope work perfectly well; I have no experience of this, but I can well believe it because spores are, compared with ordinary fossils, neat and definite units of standard form, demanding no wide knowledge for their recognition. Then they are more generally dispersed than any other kind of fossil. Think, for example, what happened to the pollen of an oak tree last summer. Most of it doubtless fell near by, but some grains will have blown far and we know that tree pollen occurs in the upper air all across the Atlantic Ocean. It all eventually falls and will be preserved in sediments everywhere—peat bogs, lake bottoms, river mouths and in the ocean far from land. Although some of these sediments will have pollen in very small quantities, we can concentrate the grains because of the special properties of their walls in resisting chemicals that destroy the rock and almost all other materials. There is no other class of fossil of which all this is true. We must recognize some disadvantages. It is all too easy to do very bad work and not be found out for a long time and some of my friends tell me they

re dismayed at the volume of bad published work that now xists. Still time has a way of dealing with that and I do not vorry. There is no doubt about the vigour of this sort of fossil otany; several times more people work in it than on ordinary ossil plants and I suppose the oil industry only employs them ecause it thinks them worth while.

Now this application of fossil botany has nothing to do with rdinary botany and it does not matter if the thing our spore eologist thinks is a pollen grain is really the egg of some minute vorm or a protozoan cyst. If it distinguishes certain rocks he an use it. It thus seems strange that these men whom I would ave expected to be the most practical-minded of geologists often how a passionate desire to be good botanists. They are bent on ecognizing true botanical species and genera and further on lassifying them in the right place in the plant kingdom, and urther on building comprehensive theories of spore evolution. And this in spite of the fact that spores are plainly rather simple hings and that very similar looking pollen grains occur in groups f diverse affinity. Think, for example, of the pollen of Podo- arpus, of Pinus, of Caytonia and of certain supposed Pteridosperms with winged grains. I only know of one group of spore eople who contentedly use their spores as fossils and no more, nd they have worked out a code number system for designating heir Types. The vehemence with which I have heard others denounce their methods reveals where their critics' hearts lie; n Botany. Plainly these would-be botanists are irritated by the mperfection of isolated spores and they are not content to be just practical geologists. I am no spore man, but if I were I dare say I would be just the same; to be practical and sensible in your job is not enough, you want to try for perfection, even if you risk making a mess.

The final application, the Botanical, has been the main thought in fossil botanists' minds since Darwin's time. They want to learn about evolution and so to solve the problems of comparative morphology and to achieve natural classification. Perhaps these should be in a different order but it doesn't matter. The greatest preoccupation of all has been with the evolution of Angiosperms, and here I can only say fossil botany has so far failed. It has had its great successes; it has established which of the ferns of to-day are of ancient families and which of compara-

tively recent appearance and by giving a general idea of direction of evolution in morphological series it greatly assisted Bower in his work on ferns; it may indeed have made a large part of it possible. But this work was largely before my time as a fossil botanist. Much more recently Florin has had great success with the Conifers, and this was through work on fossils.

The number of genera of living Conifers is not great and their variety is only moderate, but it is fair to say their classification was fluid, and the cause was very largely the result of disagreement about the female cone, in particular about the complex scales which bear the seeds. It is not merely that two extreme views were held; the number was nearer a dozen and they differed in subtle but important ways hard for most people to follow. And all depended on the evidence of comparative morphology, the same lot of facts interpreted in several ways and with different postulates. The result was chaos. It was worse; it was a nuisance to those who wanted to use classification to get on with other work, and I fancy it was a permanent source of discouragement, since no one got further by wrangling.

The part of Florin's work which had most effect was his study of Upper Carboniferous species (and they happen to be the oldest of the class). They were formerly placed in the old genus *Walchia* (now split as a result of Florin's discoveries), a familiar genus enough, but no one had looked at the cones carefully enough. Florin's diagrams of the cone scales are now familiar and I need not dwell on them. Its scale is more elaborate than in any living Conifer and is in several ways like a bract bearing an axillary leafy shoot in which certain leaves bear terminal seeds. It is also like the little seed-bearing shoots of Cordaites and here the scale leaves and stalked seeds are convincingly equivalent organs since they occupy similar places in a phyllotactic spiral. Here Florin's conclusion was considerably beyond what was the extreme view of the comparative morphology of a Pinus cone scale. In Pinus, it was indeed thought of as a bract subtending a fertile axillary organ, but most people left off there. Florin's comparisons indicate that it should comprise a stem, sterile leaves and fertile leaves, all reduced, deranged, distorted and adnate. The effect of his publication—in eight large volumes—was literally overwhelming; the alternative theories just vanished and their supporters changed their views, or if any remained unconvinced

hey stopped writing. For the first time nearly everyone viewed he Conifers in the same direction.

Would that we could do this with the Angiosperms! It could appen as the result of the study of a few well-preserved Angio- perm flowers and fruits in the Jurassic or Lower Cretaceous.

But does it really matter that we do not know the direction of Angiosperm evolution? Can we not agree to a reasonably workable and stable scheme of classification for flowering plants? Linnaeus made one which was good enough to survive for many years and everyone could understand it: very few things indeed were in doubt. The answer plainly is that we cannot. The motive of the Taxonomist who revises classification, multiplying he number of families and altering their arrangement has nothing o do with convenience, or certainly not the convenience of a ow-grade user of taxonomy like myself. His aim is perfection; and to his concept of perfection he is prepared to sacrifice everything.

I may perhaps be pardoned for digressing when I say that 'thought" in one sense of the word has been the bane of fossil botany. Fossil botanists are doing very well when they are working on a fossil, but when they write about relationships it may read well at the time, but in twenty years, how silly it seems. Indeed, I fancy some did not read well at the time and that the grievous decline in British fossil botany which happened about fifty years ago may have been caused by derision.

Now I return to our pure fossil botanist: what Holy Grail does he seek through his working life? In very large measure he is like any other botanist who is investigating a purely scientific problem, and indeed like many a scholar outside Botany and even outside science, his mind has become conditioned—or as a less sympathetic critic would say, warped, to find absorbing interest in a thing which to almost all sane men is of no interest whatever. But most of us are like that and if we do not give our minds to one thing we give them to another and we take this thing in all seriousness.

The pure fossil botanist has certain advantages. He has a rather greater chance of finding something really new than most students of plant morphology; his field is largely virgin, theirs' rather fully explored. No scientist is so pure as to despise success in discovery. At the same time he labours under a grave dis-

advantage; he can never complete his work with the perfection of ordinary morphological work. There is another factor, but whether an advantage or a drawback depends on the man, though it acts powerfully one way or the other. Fossil plant material is untidy, unexpected, everything is of uncertain interpretation, though some things are safer than others. I imagine it may be like the detective's investigation of a crime (my statements are based on light reading alone). There is a crime: the detective arrives and looks for clues and notes a large number of possible ones and there is nothing to show which will in fact lead him on and which are irrelevant. In life the number of possible clues must be infinitely greater even than in fiction, and great fun the fictional detective has before the end. And so it is in fossil botany; perhaps you are looking for clues for relating a species of fruit to a species of leaf; or perhaps something less ambitious; some clear basis for dividing a welter of leaf forms into species. The puzzle is exciting and the excitement sustains through much dull routine work. But the pleasant exercise of working at puzzles is not enough, nor is the knowledge that how far you get depends largely on the power of your brain; the excitement comes from there being at least a chance of success.

In ending this talk I thank you for inviting me. One of the best things about being invited to lecture on a named subject is that it makes you think for the first time of things which may not previously have entered your head. It is true the subject borders on philosophy and when a scientist becomes a philosopher he is usually shallow. I remind myself, too, that to attribute thoughts and motives to other men from reading their published work may be nearly intolerable conceit. I beg you to take this lecture as neither the one nor the other but as an hour's entertainment.

A Note on Some Mosses of the Lammermuir Heaths.

By Peter Harper
(Edinburgh School of Agriculture).

The first studies on this subject were concerned with the effect of single soil factors such as lime status, moisture content, humus type (Grebe, 1918; Davy de Virville, 1927) or hydrogen ion concentration (Montgomery, 1931). Most of the recent work from which information can be derived differs from these in that the mosses are not the principal subjects of study. For instance, Fraser (1940), discussing the vegetation of heathland, describes in terms of soil-habitat the distributions of several heath plants, including some mosses. Changes in the soil profile accompanied by change in the floristic composition of the vegetation have been studied by Watt (1940), working on the podzolisation of a rendzina-like chalk soil, Balme (1953), on similar features in ashwood over limestone, and Gorham (1954), studying the increase in depth of the mor humus layer in oakwood. Recent memoirs of the Soil Survey of Scotland (Mitchell & Jarvis, 1956; Ragg, 1960), provide composite species lists, which include mosses, for a number of the major soil groups.

The information given here was collected during a survey of the soils and vegetation of the Lammermuir Hills, the results of which are to be published elsewhere. Eight of the soils form part of a catena which would be found on a perfectly formed S-shaped hill slope, starting with peat on the rounded hilltop and the podzols on the gentle upper slopes. The steep mid-slopes carry scree and the brown forest soils while the gleys appear on gently sloping low-lying land adjacent the streams. The gleyed podzol occurs in similar sites to other podzols, but only over heavy clay parent material.

The table shows the distribution of fifteen common heathland mosses over fourteen soil-vegetation groups, the grass swards having been separated from heather moorland, and bracken from bent-fescue grassland in the podzols and the brown forest soils respectively.

Rhytidiadelphus loreus is confined to peat.

Sphagnum spp. are found mainly on peat, but also appear on the other podzols.

Plagiothecium undulatum is also associated with podzols.

Hypnum cupressiforme occurs on podzols and the dry brown forest series.

Leucobryum glaucum is confined to the two true podzols.

Polytrichum commune has an association with the wet soils, but returns the highest figures on podzols.

Hypnum undulatum is a plant of moist places.

Hylocomium splendens has a wide range with a preference for moisture and grassy vegetation.

Rhytidiadelphus squarrosus is another wide-ranging species, but is most frequent on the brown forest and gley soils and in grass.

Pleurozium schreberi is fairly wide-ranging, mainly amongst grass and the lower soils.

Polytrichum juniperinum is mostly found on dry soils.

Dicranum scoparium has the highest frequencies on dry brown forest soils.

Mnium hornum occurs mostly on the wet soil of the lower slopes.

Rhytidiadelphus triquetrus appears on the scree and the dry brown forest soil.

Brachythecium purum is confined to the poorly drained gley soil.

Because of the small part of the soil occupied by their rhizoids, mosses might be distributed with no reference to the soil profile as a whole, and indeed they do find niches which are suitable in many otherwise unsuitable soils. Where the upper horizons of a profile are characteristic there appears to be a marked response in the moss flora.

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Plants as Remedies: The Debt of Medicine to Botany.

Douglas Guthrie, M.D., F.R.C.S.

The age-long alliance between Botany and Medicine has come to an end this year. No longer will the first-year medical student rush sleepily to the Botanic Garden Lecture Hall in order to be in his seat by 8 a.m., when Professor Bayley Balfour will arrive and lock the door behind him. How clearly one can recall these days, although the details of the lectures have long since faded from one's memory.

Anatomy still remains the basic foundation of Surgery, but Botany is not now the basis of Medicine, as it was for many centuries.

This change is an inevitable consequence of the advance of scientific knowledge. Chemicals are used more frequently than plants as remedies, and drugs which were only obtainable from plants, are prepared synthetically by chemists.

Medicine's Debt to Botany

In the light of this changing attitude, it is only fitting that we should pay a tribute to Botany for this long and useful service, recalling what Botany has done for Medicine, and asking ourselves how this has influenced modern medicine. At the same time we must remember that the benefit has not been in one direction only. Botany has helped medicine, but medicine has also helped Botany. All the great botanists of early times were medical men. They studied botany as a whole and did not restrict their observations to plants which were of medicinal value. Botany became an exact science, a branch of knowledge, and not merely a guide to medicine or to food or to any other use to which plants might be applied. Botany grew out of medicine and medicine had its roots in botany.

During many centuries a large proportion of medicinal drugs (I add the word medicinal because the term *drug* is sometimes applied only to a sedative)—a very large number of drugs were plants, or parts or preparations of plants: many were of animal origin, and only a few were of chemical or mineral nature.

It was therefore essential that the physician should be familiar with the plants which were his stock-in-trade, his *materia medica*.

The disappearance of Botany from the medical curriculum is natural consequence of the changing attitude of modern ience. If this were all, the loss of Botany need not be much gretted.

But Botany gave Medicine something more than the cold facts science and of *materia medica*. It has ever been, in a way, an sthetic subject. Like Medicine itself, it is *an art* as well as a ience.

The "yellow primrose by the river's brim" is indeed *something* ore than just a flower, to the botanist, just as the patient, in ne eyes of the physician, is something more than an enlivened rrangement of flesh and blood. "We should count time by heart-robs", but we seldom do so.

Besides acting as a link with the Arts, and reminding us that cience cannot explain everything, Botany formed an excellent ntroduction to the study of Medicine because it assisted the tudent to acquire a logical and systematic habit of reasoning.

Taxonomy, the principle of classification so exactly applied in Botany, leads naturally to the classification and diagnosis of isease, although not, perhaps, to the extent envisaged by William ullen, who developed a system of what he called Nosology, ased upon the ideas of Linneaus.

Medicine and Botany in Partnership.

Let us now try to picture the beginnings of Medical Botany, r if you prefer it, of Botanical Medicine, and attempt to trace he progress of this close partnership. The dependence of Man pon the vegetable world is of very ancient origin, and it is ndeed an intricate and fascinating story, a many-sided tale which eals with plants as foods, and the relative food value of each, vith the diseases of plants, which present some strange analogies vith human diseases, with the diseases caused by plants, either y acting as poisons when ingested, or even at a distance, like he legendary Upas Tree, or the more familiar primulas from vhich I myself have suffered. The complete story would invade Bacteriology, and even enter the realm of the viruses, some of vhich seem to be animal, vegetable and mineral all combined and ery much alive, as enemies of man.

But all this would lead us far beyond our present subject, vhich is, the debt of Modern Medicine to the old-fashioned

Botany of yesterday, and the use of plants in the alleviation and cure of sickness.

How did it all come about, and why were plants ever used as medicines? In pre-historic times our early ancestors discovered, by the tedious and often dangerous process of experimenting on themselves, which plants were foods, which were poisons and which were remedies for diseases. Just as cats and dogs physic themselves with grasses, so did primitive man treat himself and his children. Such "folk-medicine" persists to this day. But that is not the whole story by any means. When men began to use their powers of reasoning, they did not reason in the way we might expect.

Primitive Medicine and Folk-medicine.

Primitive man did not, and does not to-day, regard disease as a natural phenomenon. In accordance with his animistic belief, he drew no distinction between body and soul. Although he dressed wounds with a leaf and soon learned the use of splints for fractures, disease was not so obviously a natural happening as was an injury. Diseases, especially those of an epidemic variety, or those which involved unconsciousness or mental disturbance, were regarded as "supernatural", the work of an enemy or an offended god who must be appeased. A demon had entered the sick person, and treatment consisted in driving it out. This was done by purging, by steam baths, by massage, by unpleasant drugs, or more often, by charms and incantations and other magical means. Perhaps our early ancestors were wiser than we are to-day, in applying treatment to the soul as well as to the body. Religion still has close affinity with Medicine. In the primitive scheme the magico-religious part of the cure was more significant than the administration of any drug. Nevertheless, the drug had its place and "folk-medicine" or domestic medicine was handed down in families through countless generations. It remains with us to the present time, and many ancient herbal remedies are still in use.

It is sometimes said that important discoveries might be made by a careful scientific investigation of the so-called "native remedies" still highly regarded by primitive people. Where it has been tried, this line of research has been very disappointing.

Many of the drugs are purgatives, but the majority have been proved to have no effect at all: their use has been entirely empiric. In Central Africa and in South America such enquiries as I have made, have led me to form a very poor opinion of the witchdoctor or *brujo*. Animal remedies, such as rhinoceros horn, viper's flesh, and powered mummy have for the most part been discarded, but leaves and roots of many plants are used, and less frequently barks and stems and flowers, generally in the form of a decoction (steeping in water) or an infusion (boiling in water). The samples vary much, according to place and season, and the dosage is random and uncertain. Now and then, a new remedy of value turns up from this source, as did *Rauwolfia serpentina* a few years ago. It is an Indian plant which has been used by native doctors since the 16th century as a sedative, and now, having been exploited as a sort of "wonder drug", and the source of reserpine and serpasil, which act powerfully, though not without danger, in the reduction of arterial hypertension. In general, native plant remedies are of little value. In 1952, Mr. Purseglove, then Agricultural Officer at Kabale in Uganda, showed me his notes of more than 1,000 plants alleged to have medicinal properties. He said that the information was unreliable, and that one native name might be applied to several different plants. Scientific analysis of the results is thus difficult or impossible. Perhaps the same may be said of the herbal cures still vaunted by herbalists in this country who, even in these days of medical science, still have a surprisingly large following.

The domestic medicine of rural districts also flourishes still. In Orkney, I was told that the root of the Buck-bean or Bog-bean (*Menyanthes trifoliata*), known also as the Craw-shoe, was often chewed by the older generation of crofters and was also given to cattle. It is used for much the same reason as Coca leaves are chewed by the natives of Peru, and Betel-nut by Indians. Also in Orkney, the leaves of Coltsfoot (*Tussilago farfara*) are smoked in a pipe and are said to cure bronchitis, while the roots of the common plant known as Thrift, when boiled in milk, will cure all chest complaints.

Each one of those medicinal plants is used in purely empiric fashion. This plant will cure that disease: the reason why, we cannot tell or even guess.

The History of Drugs and Poisons of Vegetable Origin.

Let us now look a little more closely into the history of vegetable drugs and note how their popularity rose and fell during the centuries of recorded time. I have said that in early times religion and medicine were one, and the doctor exercised a priestly function. Magic and religion played the major part in the treatment of disease.

About 460 B.C., Hippocrates, the father of medicine, arrived on the scene, and taught that there was no such thing as a sacred or supernatural cause of disease. All disease was perfectly natural, and could be cured by natural means. Our bodies, he said, were the physicians of our diseases. Nature was the great healer. Never was truer word spoken, and fortunately the Hippocratic attitude to disease remains with us still. Hippocrates used few drugs: he trusted largely to diet and regimen, and to the healing power of Nature.

Galen, who lived 600 years later, and died about 200 A.D., developed a system of medicine which lasted for more than a thousand years, and was based upon the doctrine of the humours —heat and cold, moisture and dryness. He used many drugs, and his name is perpetuated in the word "galenicals", drugs prepared from plants, as opposed to synthetic chemical remedies.

After the fall of Greece and Rome, medicine passed into the hands of the physicians of the great Moslem Empire, which extended from Persia to Spain. It may be claimed that those Arab physicians were the originators of pharmacy and *materia medica*. They introduced the processes of distillation, sublimation, and crystallisation, and discovered many new drugs. The word "drug" is of Arabic origin, as also are syrup, sugar, alcohol, and many others. During this period, sometimes erroneously called "The Dark Ages", medicine was kept alive also by the Christian Church, and in many a monastery, manuscripts were copied, and medicinal plants were cultivated.

The Revival of Learning, about the 15th century, brought new knowledge in abundance, and of course the invention of printing and the discovery of the New World each made an enormous contribution. Some of the mediæval ideas had been very curious. There was, for example, the doctrine of "signatures". For every disease, it was argued, God had provided a remedy, and the only problem was—how to find it. The clue

y in the plant itself. Saffron, with its yellow colour, was the ire for jaundice. *Pulmonaria,* which had markings on its leaves sembling the lungs, would cure lung disease. Cyclamen had a af like the human ear: it was the remedy for ear disorders. he chemists of that time were more concerned with the search or the philosopher's stone, which would turn base metals into old, than with the preparation of new remedies.

Furthermore, poisons of many kinds were used, and antidotes ere numerous. The main ingredient of the famous antidote 'heriac, was the flesh of vipers. Theriac remained in use for enturies. Indeed, it is listed in the London Pharmacopoeia of 724, and the prescription contains 62 ingredients.

Into this strange atmosphere of medicine there came 'aracelsus, a man whose work is not even yet fully appreciated. Ie focussed the attention of alchemists upon the preparation of rugs, and he greatly simplified prescribing, by seeking out the quintessence" or "active principle" of each remedy.

At a much later date, early in the 19th century, Hahnemann urther simplified matters. Whatever we may think of his inute dosage, it saved many patients from being poisoned, and is use of only one remedy at a time was a very much better dea than giving a medicine with numerous ingredients.

Even then, however, the exact action of medicines was not nderstood, and it was not until a century later, when Ehrlich ntroduced what he called "Chemotherapy" that the sky became learer. By this time it had been proved that bacteria were he causes of many diseases and Ehrlich directed his "magic ullets" to hit the mark by combining with, and neutralising the oxious agent, while avoiding injury to the tissues. Ehrlich's rinciple was carried a step farther by the introduction of enicillin, and the numerous "antibiotics" which have become so mportant in modern medicine.

Cinchona, Digitalis and Ergot.

I have referred to *Rauwolfia,* which was for many years a ative remedy, before it was adopted by scientific medicine. nother such plant was cinchona. It is said that the bark of his tree, called Quina-quina, was used by Indians in Ecuador as cure for fever. A Jesuit missionary employed it to treat the ife of the Viceroy of Peru, the Countess of Chinchon, who then

introduced it into Spain, about 1641, where it was called Jesuit's or Countess' powder. Such is the legend of the discovery. In Britain it had a great vogue, and Sir Robert Talbor made a fortune by selling it as a secret remedy. The supply ran short, and the price mounted. An Englishman, Charles Ledger, offered to sell seeds to the British Government, and when the offer was refused, sold them to the Dutch, thus inaugurating the extensive cultivation of the trees in Java, which, until recently, was the main source of the world's supply of quinine, the active principle which was isolated from the bark in 1820, and later prepared synthetically, although it has now been superseded by other drugs. When Linnaeus described *Cinchona officinalis* he omitted the first "h", and it has remained cinchona ever since.

Another folk-medicine which came into regular use was *Digitalis*. Dr. William Withering noticed that the country people of Shropshire treated "dropsy" with a concoction of 20 herbs, but the only really active ingredient was foxglove leaves. Withering tried it with success in 163 cases, and then wrote his famous treatise, "An Account of the Foxglove", in 1785, giving rules for its use, which are still followed. He also showed that dropsy might indicate heart disease. *Digitalis* has relieved many a sufferer since then.

As an example of a plant disease which can cure human disease, there is Ergot. *Claviceps purpurea* is a fungus parasitic on rye, sometimes on other cereals. Its poisonous effects were early recognised. In the 9th and 10th centuries thousands of people died during epidemics of "ergotism" which caused gangrene of the limbs and was very fatal. Since then there have been many epidemics: even as recently as 1926 in the Balkans and Russia. In modern times, it came to be used for haemorrhage after childbirth, and instead of causing deaths it saved many lives. Truly, a drug with a strange history.

Herbals and Pharmacopoeias.

A study of the ancient literature brings to light numerous interesting facts regarding vegetable remedies. Some drugs still in use, such as castor oil, are mentioned in the Ebers Papyrus, the oldest known medical book (or record) written about 1500 B.C.

Dioscorides, who lived in the first century A.D. wrote the first nown account of medicinal plants. Many similar works llowed: they were known as "herbals", and some are now very luable. One of the first to be printed was the "Hortus sanitatis", ted 1491. Illustrations in the early herbals were very crude, nt Otto Brunfels had made more accurate pictures of plants his Herbarium vivae icones, in 1530. William Turner, Dean Wells, sometimes called "The Father of English Botany", blished his Herbal in 1548, while that of Leonhard Fuchs, who ve his name to the fuchsia, appeared in 1542. Nicolas Monardes Seville set himself to describe the medicinal plants imported om Spanish America in 1569. The English translation of his ok, containing the first illustration of the tobacco plant, was ntitled "Joyful Newes out of the new-found World", 1577. The erbal of John Gerard (1636) has an illustration of the potato, en a rarity, which Gerard grew in his garden at Holborn. erard perpetuates the myth of the Goose or Barnacle tree which ore shells on its branches from which Barnacle geese hatched ut. A legend even more surprising is that of the Vegetable amb, which decorates the title-page of the herbal of John arkinson (1629). This hybrid between animal and vegetable as often illustrated, became more plant-like as time went on. arkinson called his book, "Paradisus Terrestris Paradisi in sole" The Terrestrial Paradise of Park-in-sun). A well-known writer herbalism was the notorious Nicolas Culpeper who published e Pharmacopoeia of the Royal College under his own name in 649. That Pharmacopoeia was the first official list of approved medies in English. Printed in 1618, it listed almost 2,000 medies, some of them simple, others having many ingredients. the tenth and last edition (1851), less than 300 drugs are entioned. There had been earlier Pharmacopoeias in Italy, ermany and France, and the Royal College of Physicians of dinburgh sponsored one in 1699 which continued through 14 litions. All were superseded when the General Medical Council rst issued the British Pharmacopoeia (1864), now in its 9th dition (1958).

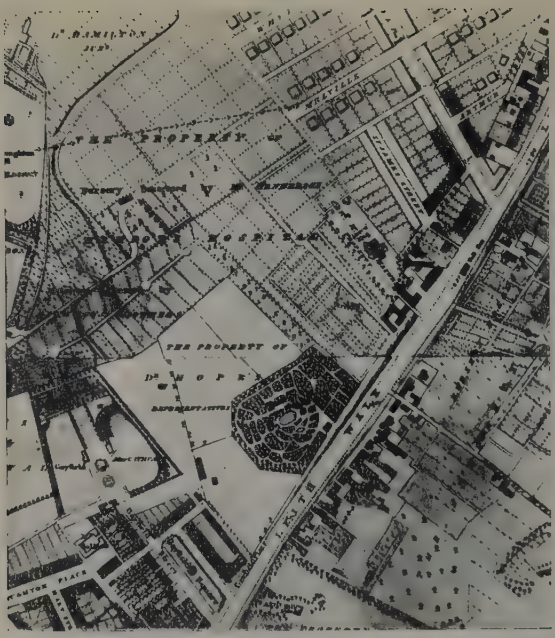
Physick Gardens in Edinburgh and Elsewhere.

When the teaching of Medicine became established in niversities and Medical Schools the need for practical tuition in

Botany became more obvious. Physick Gardens, the ancestors of modern Botanic Gardens, were established at each of the great medical centres, at Padua in 1545, Montpellier in 1593 and Leyden in 1589. The garden at Leyden was further developed by the famous physician Boerhaave, who, early in the 18th century, taught Monro and the other four professors who founded the Faculty of Medicine in Edinburgh in 1726. Boerhaave also taught Linnaeus who planted his garden at Upsala (still preserved) about 1737. Oxford had a physick garden from 1623, and the Apothecaries Garden at Chelsea dates from 1670.

Two famous physicians of Edinburgh, Sir Andrew Balfour and Sir Robert Sibbald, after consulting with Dr. Morison, Professor of Botany at Oxford, established a physick garden at Holyrood in 1670, and another in 1676 at Trinity Hospital, where the Waverley Station is now situated (see Plate III and Notes Roy. Bot. Gard. Edinb. xix, frontispiece). In charge of both gardens was James Sutherland (1638-1719), who was the first to occupy the Chair of Botany. About 1,000 plants had been collected, many of them supplied by Patrick Murray, Laird of Livingstone, and they were described or at least listed by Sutherland in his *Hortus Medicus Edinburgensis,* dated 1683, and now a rare book. The earliest of the Edinburgh physick gardens ignored by many writers, was, according to their Minutes, established by the Incorporation of Surgeons (now Royal College of Surgeons) as far back as 1656. The garden was near High School Yards, and the gardener, George Cathcart, was empowered to plant medicinal herbs and flowers "for the use of the Calling" to keep the ground clean and tidy, and to inhabit the gardener's house. He was at liberty to sell drink within the house, and also to keep "kyles" or bowls in the yard, "providing he suffer no the vulgar sort of persons and the scholars of the High School to play therat". Cathcart served the Incorporation for over 30 years and was then dismissed from office because he refused to wear the livery coat and silver badge which it had been decided that the gardener should have as a distinguishing mark. Mr. James Sutherland (he was not then professor) had been engaged to teach botany to the apprentices and members of the Incorporation at a guinea a head. The Town's College, as the University was called, also founded a small physick garden at Kirk o' Field in 1695. It is on record that a physick garden was planted a

Plan of Edinburgh showing position of the Physick Garden at Trinity Hospital.



Kirkwood's plan of Edinburgh, showing position of the Leith Walk garden.

The Vegetable Lamb, from the title-page of Parkinson's

[eriot's Hospital in 1661. Thus there were, at the end of the 7th century, no less than five distinct physick gardens in Edinurgh, and according to some accounts the Royal College of hysicians had a small private garden marked on Edgar's map Dr Rutherford's Garden". The most important of the gardens, Trinity Hospital, was removed to a site now occupied y Gayfield Square and its vicinity, off Leith Walk, in 1767, nd to the present site at Inverleith about 1820. Sutherland

Table I.

Physick Gardens of Edinburgh.

Surgeons'	1656
Heriot's	1661
Holyrood	1670
Trinity	1676
University	1695
Physicians	?1704
Leith Walk	1767
Inverleith	1822

as succeeded in 1706 by the brothers Chas. and Geo. Preston, turn, and next came Chas. Alston, who taught Materia Medica well as Botany, and was Keeper of the Garden as well as rofessor of Botany. Alston lectured on Botany in summer, om 5 a.m. to 7 a.m., and on Materia Medica in winter. In 1768 Chair of Materia Medica was established and Francis Home ecame its first occupant. Meantime the Chair of Botany was cupied successively by John Hope, Daniel Rutherford, Robert raham and John Hutton Balfour. Then followed Alexander ickson and Sir Isaac Bayley Balfour, Botany remaining a edical subject, taught by medical graduates.

Table II.

Edinburgh Chair of Botany.

James Sutherland	1695
Charles Preston	1706
George Preston	1712
Charles Alston	1729
John Hope	1761
Daniel Rutherford	1786
Robert Graham	1820
J. Hutton Balfour	1845
Alex. Dickson	1879
I. Bayley Balfour	1888
W. Wright Smith	1922
Robert Brown	1958

The Future of Medicinal Plants.

An attempt has been made in this lecture to assess the value of the service rendered to medicine by botany, and to indicate the important place which, up to the present time, botany has occupied in the history of medical progress. We have noted how chemical remedies have taken the place of medicinal plants to a very large extent. Will this trend continue? Will botany recede as chemistry advances, and will vegetable drugs become obsolete? Apparently not, because, strange to say, the demand for medicinal plants still continues. It is true that Messrs. Duncan, Flockhart & Co. no longer maintain a Physick Garden at Warriston, as they did from 1915 to 1949. On the other hand, Messrs. Ransom have a 500 acre farm at St. Ives, Hunts., and Messrs. Stafford, Allen & Co. have a large drug farm at Long Melford, Suffolk, and grow all manner of medicinal plants, as they have done for over 100 years. Evidently the day of "galenicals" is not yet past, whatever the future may hold in store.

I recently attempted to ascertain the extent to which the cultivation of medicinal plants was carried at the present time. Of course one had to begin by eliminating the plants grown or collected by the "herbalist": to confine one's attention to the regular practice of medicine, or rather to the supply of "galenicals" in modern medical practice: the natural plant as opposed to the synthetic product. I found that two of the leading manufacturers of pharmaceutical products (B.W. and Co., and D.F. and Co.), although each conducted a large drug farm at one time, had now ceased to grow medicinal plants, and this was no longer profitable. Two other firms, the main growers of drug plants in this country, kindly replied to my enquiry. S.A. and Sons, who are "probably the largest manufacturers of galenicals in this country", stated that the cultivation of drugs in Britain during the past hundred years had supplied only a small proportion of the drugs used, and this had now almost reached a vanishing point. Difficulties of wage demands, of uncomfortable work, of restricted hours, of employment of children, do not exist to such an extent in mid-Europe, which can supply plant products at a lower cost. It must be remembered that many of the drugs are used in industries, and not all by any means as medicines. Cosmetics, perfumes, flavouring agents, insecticides, absorb much of the supply. Liquorice root, for example, is largely used in making foam

re extinguishers. As for medicine, the new generation of ractitioner knows little of the old materia medica, and uses the ewer chemical drugs instead of plant remedies. The other firm, V.R. and Son, has a different story to tell. They write: "We row less medicinal crops because foreign plants are dumped here, ften below cost. In spite of this, we are carrying on, hoping that ashions will change and that galenicals will be used when some f the newer synthetic remedies have been forgotten. We still row Foxglove, Belladonna, Lavender, Aconite, Hemlock, Mint, tc., on our 500 acre farm".

Conclusion.

In conclusion, let us return to our starting point, when we aid tribute to the great service rendered to medicine by botany. The outlook in medicine has now entirely changed. Medical cience has become more and more preventive and less and less emedial. It is not surprising that chemistry has taken the place f botany in the production of drugs. Nevertheless, it seems as hough there always might remain a need for vegetable remedies, nd that chemistry cannot answer every therapeutic problem. Personally, I think it would be a pity to see botany banished *ntirely* from medicine. It is now just a small part of what is alled Biology, but we should never forget that at one time it ormed the very basis of medical education.

Notes on British Boleti.

By R. Watling.

Summary.

One new species, *Leccinum vulpinum,* a new combination, and a key to the species of the genus *Leccinum* based on habitat, microscopic and macroscopic features, are discussed. Two extralimital species, as yet unrecorded from the British Isles, *L. aurantiacum* and *L. oxydabile,* are included in the key, in the hope they may appear in the future for they may have been previously overlooked and confused with far commoner forms.

Introduction.

I have studied this genus for some five years resulting in the accumulation of large collections of dried material, spore prints and descriptions, the notes below are based on these, whenever possible. *Leccinum* is a segregate genus of *Boletus,* but despite it currently not being used in Britain it is worthy of rank as exemplified by Singer (1949). Snell (1942), Donk (1955) and others have discussed the molding on modern criteria of this old genus. It was first used by S. F. Gray (1821) in Natural Arrangement of British Plants to cover all the exannulate boleti known to him at that time. The type species selected by Murrill (1909) is Gray's first species *Boletus aurantiacus.*

Generic characters.

The following characters apply to the eight members of this genus recorded for the British Isles. The test of the genus is that it can be easily recognised in the field by the medium to large stature, absence of gluten and ring, scaly stem and pallid or whitish pores. Cap dry to slightly viscid, not mucilaginous or with viscid pellicle, tomentose, convex then slightly expanding. Cuticle often overhanging tubes being composed of filamentous hyphae, exceptionally spheropedunculate. Stem covered in mucronate scales or scabrosities, which are often dark coloured, composed of dermatobasidia, dermatoparaphyses and dermatocystidia. Flesh white, pallid, exceptionally yellow, on exposure to the air or on bruising changing to varying degrees, often blue-green in cortex of stem base, elsewhere blackish, wine coloured, steel-blue, inky, sometimes unchangeable or only faintly tinted.

Taste and smell pleasant, never acrid, rancid, etc. Pores small, whitish, or pale, hardly differently coloured from the tubes, never red, chrome yellow or purple. Tubes long, thin walled, easily separable from both pileus tissue and from each other, not splitting, free-adnate. Trama bilateral of *Boletus* subtype. Habitat associated with members of the Salicales or Fagales, exceptionally Coniferae; all appear to be mycorrhizal. Spores typically subfusoid, elongate.

Status.

Krombholzia O. Karst., 1881, frequently used in Central Europe (and its later diminutive *Krombholziella* R. Maire, 1937) and *Trachypus* Bataille, 1908, frequently used in Western Europe to cover the same group of boleti, have both been previously used, for Gramineae and Neckeraceae respectively.

Leccinum vulpinum Watling, **sp. nov.**

Pileus 30-90 mm., e convexo leviter expansus, ex rubro vulpino subniger, cacaino-tinctus, dein fusco-rubicundus vel ferrugineo-tinctus, aridus, minute tomentosus, interdum squamulis obscuri-oribus adpressis minutis fibrillosis, ad mediam partem obscurus, fere umbrinus, aliquantum asper, tactus et contusus atropur-pureus. *Cuticulus* poros impendens velum inaequale 4-5 mm. longum formans; cellulae pilei filamentosae 3·5-7μ diametro, pigmento in vacuolis distinctis obscure rubicundo partim granu-lato non continuo. *Stipes* 85-135/13-22 mm. (basi 20-28 mm.) pallidus, ad basim leviter incrassatus, robustus, completus, basi, aerugino contuso, tomentosus vel floccoso-lanatus, asper, squamulis obscurioribus decoratus, ad apicem laevior et interdum pallidior. *Squamulae* primo aliquantum albidae, dein rubicundae vel cacaino-tinctae, senectute nigrae vel umbrinae. *Tubuli* 3-11 mm. longi, adnati vel paene liberi, albidi, dein languide lilacini, secti pallide atroviolacei, ad apicem stipitis reticulum distinctum non fabricantes. *Pori* concolores, minuti, pallide cremei vel albidi, senectute leviter ochracei contusi obscuriores et leviter lilacini. *Caro* concolor, albida, interdum in pileo constans nisi lentissime incarnata, in apicem stipitis vino-tincta, in cortice ad basim stipitis aeruginea, alibi interdum sordida non fumosa, tandem sed lente pallide caesia-variegata et pallide vino-tincta. *Odor* gratus. *Sapor* subnullus. *Sporae* subfusoideae, laeves, (12) 12·5-15(15·5)/3-4μ in cumulo fuscae sed ochracco-tinctae. *Basidia* tetra-sporigera,

16·5-20 × 8-10μ. *Cystidia* ventricosa, papillata vel fusiformia, ut in *L. testaceo-scabro* et *L. aurantiaco,* 30-35/10-13·5μ ± cervice 2·3/8-10μ. Reactione $FeSO_4$ pallide virens, liquori Melzerio negativus, NH_4OH solutione phenolica et solutioni formaldehyde nullus vel leviter reactione valde pallide incarnatus.

Pileus 30-90 mm., convex, then slightly expanded, dark fox red, with cocoa-coloured tint, then deep ruddy or burnt sienna, dry, minutely tomentose, often with minute completely adpressed, fibrils, darker at the disc, possibly more umber, slightly roughened, purple sienna, when handled or bruised. Cuticle overhanging pores as irregular 'veil', 4-5 mm. in length, composed of filamentous hyphae, with intracellular pigment 3·5-7μ in diameter, rounded at the extremities ± slightly constricted at septa, dark ruddy brown pigment, in distinct vacuoles, in part granular not continuous. *Stem* 85-135/13-20 mm. (20-28 mm. at base) pallid, slightly swollen towards the base, robust, stuffed, tomentose or floccose woolly at base, which bruises blue green, rugulose, ornamented with dark scales, smoother towards the apex and possibly paler. *Scales* at first whitish, then tinted reddish brown, finally blackish or chocolate or dark brown. *Tubes* 3-11 mm. in length adnate or almost free, whitish then faintly tinted lilaceous, watery ink blue when cut, not forming distinct net at stem apex. *Pores* small, concolorous very pale cream or whitish then slightly ochraceous, bruising darker and faintly lilaceous. *Flesh* concolorous white, often unchangeable in pileus, if not, changing very slowly pinkish, wine pink in stem apex, blue green in cortex of stem base, elsewhere often sallow but not black, finally but slowly becoming patchily pale steel blue and wine pallid. *Smell* pleasant. *Taste* mild, not distinct. *Spores* subfusoid, smooth (12) 15·5-15·0(15·5) × 3-4μ, snuff brown with clay tint in mass. *Basidia* tetraspored 16·5-20 × 8-10μ. *Cystidia* ventricose, papillate or fusiform, as in *L. testaceo-scabrum* and *L. aurantiacum* 30-35 × 10-13·5μ + neck 2-3μ wide 8-10μ long. $FeSO_4$ pale greenish, Melzer's sol. negative, NH_4OH, phenol and formalin solution slight reaction, pale pinkish if any change at all. Scotland: Inverness-shire. Amongst short *Vaccinium myrtillus* in dry places, under *Pinus sylvestris,* often 2-3 individuals close together, Einich Track Wd., Rothiemurchus, 10 Sept. 1957; Loch an Eilean, Rothiemurchus, 6 Sept. 1960; Reserve Wd., Cairngorm Nature Reserve, 7 Sept. 1960 (2 collections from different

localities); Inverdruie, near Rothiemurchus, 6 Sept. 1960 (type in Herb. Kew). Material also deposited at Royal Botanic Garden, Edinburgh, and accession numbers 263-266c inclusive Watling Herbarium.

Recognised by the habitat, under *Pinus sylvestris* (*Betula* or *Populus* never seen in the vicinity), the dark dull sienna brown to fox-red pileus colour and the colour change of the flesh. It obviously belongs to the *Leccinum aurantiacum-testaceoscabrum* complex (i.e. *Boletus versipellis* auct. pl.). It has affinities to both, but differs in its close association with a member of the coniferae, in the dull colours of the pileus, lacking yellow and orange, and constantly thinner spores. The flesh also changes slowly whereas both the above species commence to change immediately on cutting. A specimen of *L. testaceoscabrum* was collected on the same day and cut along with the type collection, the latter had scarcely changed, except for the stem base, when the birch fungus had begun to change from wine lilac to the final black-blue. The pores commence whitish as in *L. aurantiacum* and the scales pass from white to reddish then finally black or brown also recalling this species. However, the lilaceous tints of the changing flesh suggest affinity to *L. testaceoscabrum.*

Singer mentions in his treatise on the Agaricales (1949) that *L. aurantiacum* is rarely encountered with *Pinus rigida,* etc., in North America; later (1959), along with Snell and Dick, he suggests, after observations carried out in Chippewa Co., Michigan, U.S.A., that this pine form seems to be constant and deserves an epithet. Tuomikoski reports similarly from collecting carried out in the Finnish pine woods; however, neither suggest a name. The material described above may be the same as the North American collections, but appears to differ in slight details (e.g. scale colour sequence), and further observations on conspecificity are required. The continental material on the other hand may be closer, if not identical. I suspect that this species will be found elsewhere in closed pinewood in the British Isles, especially in the Scottish Highlands. I first collected it in Sept. 1957, and noted its interesting habit of growth under pine; brief description of the salient points was made although the two specimens were in poor condition. Recent collections allowed further study to be carried out.

Leccinum crocipodium (Letellier) Watling, **nov. comb.**

Syn.: *Boletus crocipodius* Letellier, 1842: Fig. Champ. pl. 666.

B. tesselatus Gillet, 1874 (non Persoon, 1844): Champ. Fr., Hymen., p. 636.

B. nigrescens Richon et Roze, 1888 (non Huber, 1935): Atlas Champ., p. 191.

B. luteoporus Buchinot, 1904: apud Barb. in Bull. Soc. Mycol. France, 20, 92.

B. velenowskyi Smotlacha, 1911: Vestn. K. Ceske Spol. Nauk., 2, 60.

Krombholzia crocipodia (Let.) Gilbert, 1931: Les Bolets.

K. tesselata R. Maire, 1933: Publ. Junta Circ. Nat. Barcelona Fungi Catalunia, p. 42.

K. luteopora Sing., 1938: Rev. de Mycol., 3, 153.

Krombholziella crokipodia (Let.) Maire, 1937: Publ. Inst. Bot. Barcelona, III, No. 4, p. 49.

Leccinum nigrescens (Richon et Roze) Singer, 1947: Amer. Midland Naturalist, 37, 1.

Also *Boletus rimosis* Venturi, 1863, s. Kallenbach, s. Bresadola non Venturi, and probably *B. radicans* Rostkovius non Persoon.

Many authors probably following Singer have used the epithet *nigrescens,* erected by Richon and Roze, 1888, to cover this fungus. However, it appears that two other names had been published earlier to cover the same taxon, namely *Boletus tesselatus* Gillet, 1874 (preoccupied) and *Boletus crocipodius* Letellier published some thirty-two years earlier. *Boletus nigrescens* has been used on the understanding that there is no adequate description to accompany Letellier's excellent plate. Thus in 1938 Singer supported the epithet *luteoporus* Buchinot. This was later reduced to a synonym of the earlier name *nigrescens* when this boletus was taken up in the genus *Leccinum, Boletus crocipodius* being cited as though a *nomen nudum.* The name *nigrescens* has also been used much later by Huber to cover a different bolete, now known to be *Leccinum carpini* adequately redescribed by Pearson (1946a).

Gilbert has shown the valid epithet for this fungus is *crocipodius,* the only representative of Section *Luteoscabra* Singer, 1947, of the genus *Leccinum* to be found in Western Europe. The

ate A. A. Pearson (in litt. and 1946a) has said that many epithets have been applied to this fungus, each with some point which invalidates its priority. Letellier's epithet is based on a good plate figure. Many French authors have followed Gilbert's lead. There seems to be some disagreement on anatomical features between Romagnesi and Singer's collections and further study is required. A plate and description is given by C. Rea (Trans. Brit. Mycological Soc., 1912).

The type for the transfer to *Leccinum* of Letellier's fungus is that accepted for the original combination *Boletus crocipodius*.

FIELD KEY TO GENUS LECCINUM

In the following key two species as yet unrecorded from the British Isles are included. This is because they occur quite well distributed on the continent and may have been previously overlooked in Britain or confused with commoner species, which in many details they resemble. They appear, as *L. crocipodium* to prefer warmer woodland areas and so may be met with in the future in the South of England. *L. oxydabile* may be easily misidentified as *L. scabrum*, and *L. aurantiacum* was formerly classed along with *L. testaceoscabrum* under the names *Boletus versipellis* and, more uncommonly in this country, *B. rufus*. S. F. Gray's description *L. aurantiacum β leucopoda* suggests that the true *L. aurantiacum* is to be found in Britain as this description approaches more *L. aurantiacum* than *L. testaceoscabrum*. Fresh collections are required, however, to confirm its position in our flora, although F. B. Hora (in litt.) has collected a fungus from under aspen and birch very recently in the south of England which appears to be close to, if not the same as, *L. aurantiacum*.

1. Tubes yellow and with olivaceous tint to the spore print. Pileus ochre, tawny olive or yellowish, often cracking, tomentose. Stem pale yellowish with small yellow or grey scales. Flesh yellowish white turning directly blackish or becoming first reddish, then finally black, possibly tinted brownish. Under *Quercus/Fagus*.

   L. crocipodium (*Letellier*) *Watling*

1. Tubes not yellow and with no dominant yellow colours on stem, cap or in the flesh. Without olive tint in the spore print.

2. Pileus white—very pale buff, often, especially when mature, with glaucous green cast. Stem white or greyish, with small white scales, rugulose, slender. Flesh white, unchangeable except at the cortex of the base of the stem, where it changes blue-green. In *Sphagnum bogs under Betula pubescens.*

L. holopus (*Rostk.*) *Watling*

2. If pileus white, never with greenish colouration and flesh immediately changing brownish or blackish. If flesh unchangeable ± blue green in the stem base, and pileus of another colour 3

3. Pileus whitish-pallid flesh colour then tinted ± stronger ruddy. Stem robust with large floccose white scales. Flesh white turning immediately lilacaceous, ruddy brown, then black purple, finally blackish-brown ± blue green at the base of the stem. Amongst *Molinia caerulea,* under *Pinus sylvestris*/*Betula* spp.

L. percandidum (*Vassilkov*) *Watling*

3. Not so. If pileus pallid or pale, flesh unchangeable, otherwise pileus strongly coloured and scales often blackish-brownish 4

4. Pileus fox-red, rusty brown then a more burnt sienna, dull fibrillose streaky esp. towards the margin. Flesh blue green at base of stem in cortex and slowly flushing lilacaceous or brownish at the apex of stem + patchily faintly steel blue. Stem ornamented with dirty white, then ruddy brown, finally dark brown to black, scales. Amongst *Vaccinium myrtillus,* under *Pinus sylvestris.*

L. vulpinum Watling

4. If pileus approaching tawny fox-red, then flesh changing immediately and intensely. Habit not under *Pinus* spp. 5

5. Pileus tawny orange, orange brown or bright orange red, flesh changing 6

5. Pileus more sombre without trace of tawny orange, flesh either changing or not 7

6. Pileus relatively dull red orange, brownish orange red, min. tomentose. Stem whitish with white scales, which turn reddish orange, finally red

brown or dirty orange. Flesh sallow turning slate black, without lilacaceous tint. Pores commencing whitish. Under *Populus tremula.*

L. aurantiacum (*Bulliard ex Fries*) *S. F. Gray*

6. Pileus yellowish tawny, orange brown or yellowish, min. tomentose. Stem robust with large black or very dark brown scales. Pores commencing greyish or slightly pale brownish. Flesh white turning lilac, wine colour, inky blue-black, finally blackish, greenish or blue green at base of stem. In scrub, coppice or open woodland under *Betula verrucosa* or *B. pubescens.*

L. testaceoscabrum (*Secretan*) *Singer*

7. Flesh changing some shade of black or grey, usually very strongly 8

7. Flesh not changing black, if changing, then faintly flushed pinkish 9

8. Flesh white turning salmon pink, then blackish, possibly greenish at base of the stem. Pileus cinnamon buff, then more brown, cuticle projecting beyond the adnate tubes, aspect stippled. Stem robust, white then greyish often greenish at the base with black scabrosities. Under *Populus* spp. rarely *Betula* spp.

L. duriusculum (*Schulzer*) *Moser apud Gams*

8. Flesh white to pale yellow turning reddish or violet, then grey, finally black, not blue green in stem base. Pileus buff, snuff brown or tawny olive, usually cracking. Pores cream buff with ± slightly yellow cast. Tubes free projecting beyond the cuticle. Stem, slender, white or yellowish grey, deeply sulcate with greyish or black scales. Cuticle of pileus composed of globose cells 10-12 μ in diameter. Under *Carpinus/Corylus.*

L. carpini (*R. Schulz ex Pearson*) *Moser apud Gams*

9. Pileus greyish, brown buff, sepia 10

9. Pileus differently coloured, either pale buff, pallid or umber-vandyke brown, never very large, up to 60 mm. 11

10. Flesh hard, white ± pale citron yellow in stem, reddening slightly when exposed to the air. Pileus ochraceous greyish brown, blackish often cracked, cuticle containing hyphae often exceeding 10μ in diameter and cylindrical in shape. Stem white pallid, with grey, then black squamules. Dermatoparaphyses voluminous, very few if any unpigmented. Flesh with Fe SO_4 bluish, green in yellowish parts of stem, HCHO distinctly reddish. Majority of spores greater than 5·5μ in width. Under *Betula* spp. in open places, with widely scattered trees.

L. oxydabile (*Singer*) *Singer*

10. Flesh soft, white unchangeable except for perhaps a faintly perceptible pinkish flush at apex of stem. Pileus grey, brown or yellow brown, cuticle containing hyphae in the main 4-7μ in diameter and attenuated at the end. Stem medium or slender with small brown or black scales. Dermatoparaphyses not voluminous and not always pigmented. Flesh with Fe SO_4 pale blue grey, HCHO pale pinkish. Majority of spores not or hardly exceeding 5·5μ in width. Under *Betula* spp. in coppice, scrub and open woodland.

L. scrabrum (*Bulliard*) *S. F. Gray*

11. Cap very dark brown, umber or vandyke brown, often almost black. Stem medium, rarely slender with black, brown or dark greyish scales. Flesh never blue green, unchangeable or perceptibly pinkish. Under *Betula* spp. in coppice or open woodland.

Near if not identical with *L. scabrum* (*Bulliard*) *S. F. Gray*. Requires further observations in the field and laboratory.

11. Cap white, very pale buff or pallid, never tinted either reddish or greenish, possibly becoming faintly straw, minutomentose, not viscid. Stem medium with greyish, brown or blackish scales. Flesh never blue green at base of stem white not usually flushing faint pink in stem apex. Under *Betula* spp. in open woodland.

Near if not identical with *L. scabrum* (*Bulliard*) *S. F. Gray*. Requires further observation.

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An Investigation of Mixed Populations of Primula veris and P. vulgaris.

By Alison B. Mowat.

In the East Neuk of Fife, *Primula veris* L. occurs much less frequently than the widespread *P. vulgaris* Huds. Within this area (the Ordnance Survey 10 Km. square 37/61) *P. vulgaris* is uniform, but *P. veris* is more variable. In certain localities plants superficially like *P. veris* exhibit some of the characters of *P. vulgaris* and other plants occur which appear intermediate between the two species. It was suspected that introgression might have occurred although in other populations Clifford (1958) was unable to detect it by his statistical techniques.

The Primula populations of three areas, approximately 10 × 12 yards, were studied. One was a mixed population with both *P. veris* and *P. vulgaris* occurring; the second was mainly a population of *P. veris,* but with some anomalous plants, and was sited about 20 yards from any typical *P. vulgaris*; the third was a population of *P. vulgaris,* several hundred yards away from any *P. veris* plants.

These populations were examined as follows:—

Ten pairs of characters which most readily differentiated the two species were selected, and each plant was scored in the field. The scoring was adjusted in such a way that a typical *P. veris* received the maximum score of 10, and a typical plant of *P. vulgaris* the minimum of 0.

The ten characteristics of the two species chosen are listed in Table 1.

Table 1.

Characters used for analysis of Primula species.

Primula veris L.		*Primula vulgaris* Huds.
Leaves finely pubescent on both sides.	1.	Leaves pubescent beneath, glabrous above except on veins.
Leaves abruptly contracted.	2.	Leaves gradually narrowed.
Petiole as long as blade.	3.	Petiole short.
Inflorescence pedunculate.	4.	Inflorescence basal.
Flowers nodding.	5.	Flowers ascending.
Calyx finely pubescent.	6.	Calyx with shaggy hairs.
Corolla strongly concave.	7.	Corolla flat (or not strongly concave).
Corolla 10-15 mm. in diameter.	8.	Corolla more than 15 mm. in diameter.
Corolla deep yellow or buff.	9.	Corolla pale yellow.
Corolla with orange lines or spots.	10.	Corolla without orange markings.

The results of the field scoring may be expressed diagrammatically by the method of Fassett and Calhoun (1952), which is essentially a simplification of that first suggested by Wilmott (1950), or the method of hybrid indices due to Anderson (1936). The results using this latter method are illustrated in Figs. 1a and 1b.

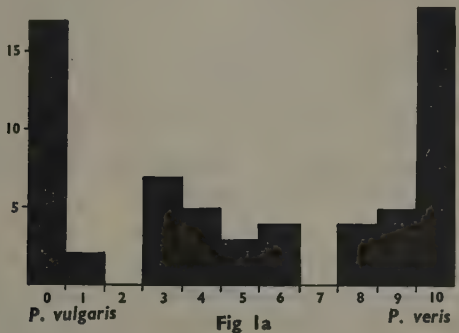

Fig 1a

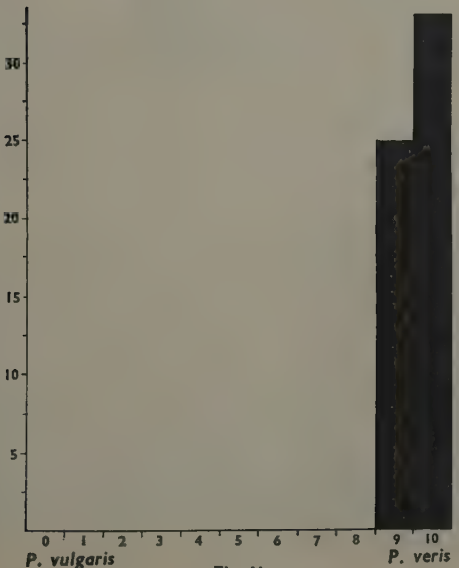

Fig 1b

Fig. 1a shows the composition of a sample of 65 plants of the mixed *P. veris* and *P. vulgaris* population. It can be seen that of the total number of specimens, only 54% can be referred unequivocally to either species, the remaining 46% being intermediate in varying degrees.

The second population, samples of 58 plants, comprised *P. veris* and some anomalous plants, is illustrated in Fig. 1b. In this instance, 43% of the plants differ from the *P. veris* standard by a single character but this varied from plant to plant, divergence occurring in the posture of inflorescence, degree of concavity of the corolla, corolla colour and the presence or absence of orange markings.

In the third population the sample (c. 60) conformed completely to the chosen *P. vulgaris* standard.

Discussion.

British Primulas have been extensively studied by Valentine, and the following is a summary of some of his findings concerning *P. veris, P. vulgaris* and their derivatives (Valentine, 1955).

(i) The cross, *P. veris* ♀ × *P. vulgaris* ♂ results in the formation of good seed with up to 37·5% germination. The reciprocal cross, *P. vulgaris* ♀ × *P. veris* ♂ gives only non-viable seed. F_1 hybrids, therefore, are only formed when *P. veris* is the seed parent. The F_1 when selfed does produce an F_2 generation but with a low seed yield.

(ii) The backcross *P. veris* ♀ × *P.* (*veris* × *vulgaris*) ♂ sets good seed with up to 75% germination.

P. vulgaris ♀ × *P.* (*veris* × *vulgaris*) ♂ also produces good seed with up to 41% germination.

The reciprocal backcrosses apparently resulted in seed yields of about 20%.

In the light of Valentine's experiments and the observed distribution of the two species, it seems reasonable to suggest that the composition of the three populations may be accounted for in the following ways.

The mixed population, on an exposed cliff at 37/616110, contained *Primula veris* and *P. vulgaris* plants to the extent of 54%, while the remaining 46% was made up of intermediates (cf. Fig. 1a). As both parents occur together, F_1 hybrids *P. veris* × *vulgaris* would be expected. There is also the possibility of the backcrossing of this hybrid as pollen parent on either *P. veris*

r *P. vulgaris*. From the experimental results of Valentine, seeds rom the backcross *P. veris* ♀ × *P.* (*veris* × *vulgaris*) ♂ would e expected to be the more viable. A proportion of both parents, oo, would also breed true.

The population did, in fact, appear to bear out these predic- ions. As shown in Fig. 1a between *P. veris* and *P. vulgaris* is a range of intermediate forms. Those with scores from 3 to 6 probably represent F_1 hybrids, while those with scores 1 and 8-9 may well represent F_2 backcrosses on to each parent. It is apparent, too, that the suggested backcrosses on to *P. veris* (scores 8 and 9) exceed those on to *P. vulgaris* (score 1), their ratio being 4·5 to 1. This may reflect Valentine's suggestion that the backcross *P. veris* ♀ × *P.* (*veris* × *vulgaris*) ♂ produces a larger proportion of viable seed.

The gaps which occur between these groups of scores cannot be accounted for readily. They may, in fact, represent discontinuities in the series, or they may be spurious and might have been obviated had other characteristics been chosen for study. For instance, scape length was observed to be variable and is probably polygenically controlled (Valentine, 1953) but in this population the degree of exposure also affected its expression. Some plants, which in other respects were typical examples of *P. veris,* had scape lengths of only 8 cms., the normal being quoted as 10-30 cm. (Clapham, Tutin and Warburg, 1952). In the two other areas, conditions were less rigorous, and an average scape length of 15-20 cm. was obtained in the predominantly *P. veris* population.

The second population, at 37/609116, again near the shore, but in a more sheltered position, contained apparently *P. veris* plants of which, however, 43% exhibited a single *P. vulgaris* character (cf. Fig. 1b). The distance between this population and *P. vulgaris* (about 60 feet) is not too great to preclude the possibility of rare hybridizations. Crane and Mather (1943) and Bateman (1947) have shown that in insect pollinated plants the relationship between contamination and distance is not linear. Bateman has demonstrated that in such insect pollinated species as turnip and radish, separation of 100 feet resulted in contamination of the order of 5-1%, but beyond 150 feet it fell to about 1%. These figures were obtained under conditions most favourable to contamination but in unfavourable conditions it may fall to

1% at only 15 feet (Mather, 1946). Since only *P. veris* × *P. vulgaris* produces viable seed, backcrosses within this population can only be *P. veris* ♀ × *P.* (*veris* × *vulgaris*) ♂, which will produce good seed with a relatively high percentage germination. The ultimate result would presumably be a superficially pure *P. veris* population with, however, some plants possessing one or more features for *P. vulgaris*. The results in Fig. 1b may be interpreted in this sense, score 10 representing the pure *P. veris* and score 9 that part of the population derived from *P. veris* ♀ × *P.* (*veris* × *vulgaris*) ♂ plants.

The third area, by the shore at 37/610114, is composed of pure *P. vulgaris* and is over 900 feet away from any *P. veris* plants. It is not impossible that cross-pollination might occur, but within the colony it would be *P. vulgaris* ♀ × *P. veris* ♂ which, as Valentine has demonstrated, does not produce viable seed; so that a pure population of *P. vulgaris* would be expected. This is borne out by observation.

In the first two populations hybridization between *Primula veris* L. and *P. vulgaris* Huds. has occurred and subsequently introgression, the extent of which has been determined by the opportunity of cross-pollination taking place.

In the mixed population backcrossing of hybrid plants has occurred to both *P. veris* and *P. vulgaris,* since both parents and their F_1 hybrids are found in close proximity. The resulting colony is very variable and shows gradation between the two species.

In the superficially *P. veris* population, backcrossing has only taken place between the F_1 and *P. veris*. No F_1 plants were, in fact, found so that they presumably occurred rarely and the only trace of their existence is now the introgressant *P. vulgaris* characters in the predominantly *P. veris* population.

The last population of *P. vulgaris* was isolated from *P. veris* both by distance and the fact that the cross *P. vulgaris* ♀ × *P. veris* ♂ is inviable.

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Plants of Duddingston Loch Bird Sanctuary.

By J. Grant Roger.

Perhaps the best general view of the Sanctuary with its associated vegetation is obtained by looking eastward across the loch from the southern slopes of Arthur's Seat. From here the distribution and range of the main ecological zones can be seen to advantage, especially the great reed bed or reed swamp which forms the most definite and conspicuous plant community of the whole area. This reed swamp occupies some twelve acres at the western end of the loch and along a considerable part of its southern shore with much smaller extensions at the east end where there is a marsh of some three and a half acres. Behind the reed swamp, on the southern side, there is an area, originally of damp meadow land, now largely occupied by introduced trees and shrubs (native and exotic), giving additional shelter to resident and visiting birds. The northern shore of the loch rises more steeply and has generally an open margin or with only comparatively narrow belts of reeds and sedges.

The flora of the Sanctuary may perhaps be best considered by grouping species according to their habitats, proceeding landwards from the open water of the loch.

1. *Aquatic Plants.*

(a) *Submerged or mainly submerged plants.* This group includes Autumnal Starwort (*Callitriche autumnalis*), Common Hornwort (*Ceratophyllum demersum*), Mare's Tail (*Hippurus vulgaris*), Spiked Water Milfoil (*Myriophyllum spicatum*), Slender-leaved Pondweed (*Potamogeton filiformis*), Fennel-leaved Pondweed (*P. pectinatus*), Small Pondweed (*P. pusillus*), Water Crowfoots (*Ranunculus circinatus, R. trichophyllus*), and Horned Pondweed (*Zannichellia palustris*).

(b) *With floating leaves.* Gibbous Duckweed (*Lemna gibba*), Lesser Duckweed (*L. minor*), Fringed Waterlily (*Nymphoides peltatum*), Floating Persicaria (*Polygonum amphibium*), Broad-leaved Pondweed (*Potamogeton natans*), Water Crowfoots (*Ranunculus baudotii, R. hederaceus* and *R. peltatus*).

Besides the flowering plants mentioned under (a) and (b) above, there are in the waters of the loch many species of multi-

cellular and unicellular algae which require investigation. The unicellular forms (including desmids, diatoms and flagellates) constitute the bulk of the phytoplankton population.

2. *Plants of the Reed Swamp.*

The Common Reed (*Phragmites communis*), which is the dominant species of this zone, occurs in dense ranks with flowering stems usually ranging in height from 6 to 9 feet. In places it is closely associated with the Great Pond Sedge (*Carex riparia*) which occurs in compact colonies, often to the water's edge. Alders (*Alnus glutinosa*) are prominent here and there in the Reed Swamp, evidently representing the relicts of a more extensive alder woodland, and about the landward edges of the swamp there are several willows. Other species of this community include: Water Plantain (*Alisma plantago-aquatica*), Great Hairy Willow-herb (*Epilobium hirsutum*), Water Horsetail (*Equisetum fluviatile*), Yellow Iris or Flag (*Iris pseudacorus*), Water Whorl Grass (*Glyceria maxima*), Bogbean (*Menyanthes trifoliata*), Branched Bur-reed (*Sparganium ramosum*) and Great Reed Mace (*Typha latifolia*).

3. *Marsh Plants.*

Where the reed swamp and the marsh land meet on the south and east sides of the loch, rushes (chiefly *Juncus effusus*) are locally prominent, sometimes associated with the Yellow Iris, Bur-reeds and the Great Pond Sedge, while in shallow water the Mare's-tail is often abundant, along with the Water Horsetail.

Since the marshy area in general comprises small pools and ditches and merges with the adjoining damp meadowland, its vegetation is rich in species, among which are the following:—

Marsh Foxtail (*Alopecurus geniculatus*), Fools' Water Cress (*Apium nodiflorum*), Lesser Water Plantain (*Baldellia ranunculoides*), Narrow-leaved Water-parsnip (*Berula erecta*), Nodding Bur Marigold (*Bidens cernua*), Trifid Bur Marigold (*B. tripartita*), Broad-fruited Water Starwort (*Callitriche stagnalis*), Spring Water Starwort (*C. verna*), Marsh Marigold (*Caltha palustris*), Lady's Smock (*Cardamine pratensis*), Lesser Pond Sedge (*Carex acutiformis*), Carnation Sedge (*C. panicea*), Black Sedge (*C. nigra*), Beaked Sedge (*C. rostrata*), Marsh Thistle (*Cirsium palustre*), Great Hairy Willow-herb (*Epilobium hirsutum*), Common Spike Rush (*Eleocharis palustris*), Marsh Horsetail (*Equisetum*

palustre), Marsh Bedstraw (*Galium palustre*), Flote-grass (*Glyceria fluitans*), Jointed Rush (*Juncus articulatus*), Common Rush (*J. effusus*), Hard Rush (*J. inflexus*), Ragged Robin (*Lychnis flos-cuculi*), Water Mint (*Mentha aquatica*), Tufted Water Forget-me-not (*Myosotis caespitosa*), Water Forget-me-not (*M. palustris*), Water-cress (*Nasturtium microphyllum*), Reed Grass (*Phalaris arundinacea*), Marsh Cinquefoil (*Potentilla palustris*), Lesser Celandine (*Ranunculus ficaria*), Lesser Spearwort (*R. flammula*), Great Spearwort (*R. lingua*), Creeping Buttercup (*R. repens*), Celery-leaved Crowfoot (*R. sceleratus*), Sharp Dock (*Rumex conglomeratus*), Marsh Ragwort (*Senecio aquaticus*), Chickweed (*Stellaria media*), Bog Stitchwort (*S. uliginosa*), Stinging Nettle (*Urtica dioica*), Water Speedwell (*Veronica anagallis-aquatica*), Brooklime (*V. beccabunga*), Marsh Speedwell (*V. scutellata*).

4. *Meadow Plants.*

There is naturally some overlap among the species of the marshland and the damp meadowland, but the following are among the most prominent plants in the latter habitat: Milfoil (*Achillea millefolium*), Fiorin (*Agrostis stolonifera*), Oat-grass (*Arrhenatherum elatius*), Musk Thistle (*Carduus nutans*), Cock's foot (*Dactylis glomeratus*), Tufted Hair-grass (*Deschampsia caespitosa*), Hogweed (*Heracleum sphondylium*), Yorkshire Fog (*Holcus lanatus*), Annual Meadow-grass (*Poa annua*), and the Broad-leaved Dock (*Rumex obtusifolius*).

Several weed species from the neighbouring arable and waste ground (e.g. Groundsel (*Senecio vulgaris*) and Feverfew (*Chrysanthemum parthenium*)), frequently appear about the edges of the Sanctuary.

5. *Woodland Plants.*

Many species of trees and shrubs, British and alien, are established in the woodland area along the south side of the Sanctuary. The larger trees include Sycamore (*Acer pseudoplatanus*), Horse-chestnut (*Aesculus hippocastanum*), Alder (*Alnus glutinosa*), Hornbeam (*Carpinus betulus*), Beech (*Fagus sylvatica*), Ash (*Fraxinus excelsior*), Scots Pine (*Pinus sylvestris*), Wild Cherry (*Prunus avium*), Grey Poplar (*Populus canescens*), Black Poplar (*P. nigra*), Black Italian Poplar (*P. serotina*), Black Cottonwood (*P. trichocarpa*), Pedunculate Oak (*Quercus robur*), Sessile Oak (*Q. petraea*), White Willow (*Salix alba*), Goat Willow

(*S. caprea*), Crack Willow (*S. fragilis*), Bay-leaved Willow (*S. pentandra*), Common Osier (*S. viminalis*), White Beam (*Sorbus aria*), Common Lime (*Tilia* × *europaea*), Field Elm (*Ulmus procera*), and Wych Elm (*U. glabra*).

Of these trees the poplars and willows are most conspicuous, and well adapted to their habitats along the margins of the loch and its adjoining wet land. The alders, and a few willows, extend well beyond the woodland, into the reed swamp.

Among the smaller trees and shrubs are Birch (*Betula verrucosa*), Dogwood (*Cornus sanguinea*), *Cotoneaster horizontalis, C. simonsii,* Hawthorn (*Crataegus monogyna*), Holly (*Ilex aquifolium*), Privet (*Ligustrum ovalifolium* and *L. vulgare*), *Lonicera deflexicalyx,* Bramble (*Rubus fruticosa*), *Rhododendron ponticum,* Elder (*Sambucus nigra*), Snowberry (*Symphoricarpus albus*) and *Syringa yunnanensis.*

A number of species from the neighbouring marshy ground and reed swamp appear in the woodland area, especially in and by the ditches, but the following occur on the drier land among the trees: Belladonna (*Atropa belladonna*)—very local, Tufted Hair-grass (*Deschampsia caespitosa*), Broad-buckler-fern (*Dryopteris austriaca*), Male Fern (*D. filix-mas*), Herb Robert (*Geranium robertianum*), Hogweed (*Heracleum sphondylium*), Wood Millet (*Milium effusum*), Reed-grass (*Phalaris arundinacea*), Creeping Buttercup (*Ranunculus repens*), Broad-leaved Dock (*Rumex obtusifolium*), and Hedge Woundwort (*Stachys sylvatica*).

Apart from the five main habitat areas referred to above there is within the Sanctuary a steep rocky slope overlooking the north-east end of the loch. Here the prominent woody plants are Hawthorn (*Crataegus monogyna*), Ivy (*Hedera helix*), Bramble (*Rubus fruticosus*), Whin (*Sarothamnus scoparius*), Elder (*Sambucus nigra*), White Beam (*Sorbus aria*), and a few willows near the loch; and among the more common herbs are Milfoil (*Achillea millefolium*), Bent Grass (*Agrostis* spp.), Early Hair-grass (*Aira praecox*), Cock's foot (*Dactylis glomerata*), Sheep's Fescue (*Festuca ovina*), Dove's-foot Cranesbill (*Geranium molle*), Timothy (*Phleum pratense*), Wood Sage (*Teucrium scorodonia*), and Thyme (*Thymus drucei*).

On the wall between the reed swamp and the rocky slope Wall Rue (*Asplenium ruta-muraria*) is abundant.

Compositae and the Study of Functional Evolution.

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The capitulum in action.
The contrast of capitulum and single flowers.
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PREFACE.

The challenge of Compositae lies in an apparent paradox o their evolution. Two characteristic features have been held primarily responsible for the large size of the family and its world-wide distribution: they are the capitular inflorescence o numerous flowers and the pappus, which equips the fruit fo dispersal by wind. Yet within Compositae the evolutionary trend seems, in a number of independent lines, to be towards reductio of the capitulum to a few flowers, or even one, or towards th loss of the pappus. This paradox has provoked a good many "explanations", some of which lead down paths of morphological philosophical thought where the practical investigator canno follow. Yet the great need in Compositae is for practical studies The purpose of this article, then, is to criticise some of thes theories, to look again at the capitulum as a functional unit, an to suggest some lines of investigation which may lead to a bette appreciation of the family as a whole and of the factors affectin its evolution. All this is treated in the most introductor manner: the subject is one for a book.

THE CAPITULUM AND ITS VARIETY.

Troll (1928, 1957) calls the capitulum a "pseudanthium"*,

*This use of the term for an organized aggregation of individual flowe is not to be confused with the theory of the pseudanthic natur of the flower itself which was put forward on a limited front b Delpino (1892) and elaborated by Wettstein (cf. Zimmermann 1959, p. 497).

'alse flower, and many writers, both before and since the intro-'luction of this term, have said that the head of a composite is ›iologically equivalent to a single flower. Common speech 'eference to a daisy or marigold flower and the technical use of :he term floret (*flosculus*) for the individual flowers have encouraged this view, which is to be found in the writings of Wernham (1912, p. 295), Philipson (1957), Danser (1950, p. 158), Good (1931, 1956), Leppik (1960), and many others. Corner (1949, p. 388; 1958, p. 33) has added his own characteristic descriptive note that the capitulum may be regarded as develop-ng by transference of the function of the individual flower to the inflorescence†.

Biological equivalence is too slippery a concept to be worth argument. Throughout this paper the term flower means the ndividual flower, not the flower head. The questions we have to ask are, first, what happens in the composite capitulum, and, econdly, is there any marked contrast therein compared with events in a solitary flower.

No complete analysis of the very great variety in the structure of the capitulum has yet been made. Good (1956, p. 297) has ecognized seven of the "more prevalent" patterns, but this is a nere morphological outline of the individual head; it takes no account of function (with respect to pollination, for instance) or he sex-distribution of the flowers, nor of the size of the head or ts arrangement in the secondary inflorescence. Good's "dande-ion pattern" includes not only the many-flowered erect head of dandelion (*Taraxacum*) or sow-thistle (*Sonchus*), but also the ruly flower-like 4-flowered head of *Lactuca orientalis* and the pendulous 3-flowered capitula of *Prenanthes purpurea.* The dandelion would be classed by Leppik (1960) as a haplomorphic ype, *Lactuca orientalis* as a pleomorphic type; these types being part of a series distinguished according to the pattern of ecognition-outline which they present to visiting insects. Leppik's

†Corner's general concept of transfer of function puts into morpho-logical terms the kind of change that takes place when there is an advance or delay in the time or position in which the action of a particular gene or gene-complex comes into play. In most of the examples he cites I believe it to be a valid concept, but I doubt if it can be applied to the composite capitulum. There is superficially a morphological transfer, but it is scarcely explicable in the same genic terms, and on further consideration is seen to be only superficial.

system is, however, too narrow for a general classification of capitula.

After flowering is over the capitulum is intimately concerned with, and plays a varying part in, fruit-dispersal. Fruiting behaviour may differ in capitula that are of the same pattern at flowering time; for example, some *Crepis* heads are xerochasic, opening when dry, whereas *Cichorium* may be hygrochasic, opening when moist. Other members of the *Cichorioideae* with similar capitula at the flowering stage, become synaptospermous in fruit; that is to say the achenes are held within the indurated capitulum and the whole is dispersed as a several-seeded disseminule (*Hedypnois cretica* forms—Zohary, 1950; cf. Murbeck, 1920, 1943). In lettuce (*Lactuca*) the wild species have involucral bracts that spread in the fruiting stage and the seeds are freely dispersed; in cultivated forms a single recessive gene keeps the bracts erect and the seeds are retained in the head (Whittaker & McCollum, 1954). Such may be the origin of more elaborate forms of synaptospermy. The classifications of the flowering and fruiting stages of the capitulum may need to be kept distinct; yet the requirements of the two stages will certainly inter-act.

THE CAPITULUM IN ACTION

The chief functional characteristic of a composite capitulum is the presentation, over a relatively long period, of a succession of stigmas to separate acts of pollination, each of which leads to the fertilization of one ovule. Such a system gives opportunity in a single head for the production of seed which has been developed by cross-pollination from several different pollen parents.

A convenient subject for an elementary experiment was *Callistephus chinensis*. This plant has female ray-flowers and a flat-topped disc of hermaphrodite flowers. First the female ray-flowers open, before any pollen is available in the same head; there is thus an opportunity for them to be pollinated from another plant (or from a different capitulum on the same plant). Next the outermost of the hermaphrodite disc-flowers open; they are protandrous and the pollen is swept up out of the anther-tube by the protrusion of the style*. Each day further disc-

*Details of the pollination mechanism of Compositae have been given on numerous occasions and there is no need to repeat them here. For details and summary, see Small (1915, 1919).

flowers open in the male stage and those already expanded pass into the female stage by the separation of the stigmatic arms.

Several true-breeding horticultural colour forms were obtained and planted up so that a white-flowered plant was in the centre. After flowering, all the ripe seed was collected from one of the white-flowered capitula and was sown next year. When the family came to flower it included not only numerous white-flowered plants but also representatives of all the half-dozen colour forms which had been growing around it. *Callistephus* is self-fertile, which accounts for the large number of white offspring (only about 10% out-crossing is normal: Wit, 1936); many Compositae are self-incompatible (for list see Fryxell, 1957, 168-173) and, for these the potential range of pollen-parents would be even greater.

The period over which flowers are opening in any one capitulum varies, of course, according to the species (and weather conditions), but here are a few sample records made at Edinburgh in 1956: —

Species	Number of flowers in head	Duration of head
Eupatorium riparium	23	11 days
,, raffillii	101	13 ,,
Senecio heritieri	12 + 104	9 ,,
Anthemis montana	21 + 217	19 ,,
Doronicum caucasicum	30 + 203	14 ,,
Olearia myrsinoides	5 + 10	10 ,,

These merely give an indication of what happens. Where the number of flowers in the head is split into two figures, the first refers to ray-flowers, the second to the disc. The duration of the head is from the opening of the first flower to the opening of the last; not to fading. Figures are averages of a small number of heads: a full quantitative study would require many more observations than have been made so far, and should include notes on the spatial separation of the newly opened flowers. This may be important in large capitula, which open relatively faster than small ones.

Details of the daily march of events are given below for three species: the ray-flowers of *Doronicum* and *Anthemis* all open first and are ignored. It will be seen that the rate of opening is quite erratic. We have not yet made any records of the duration of receptivity of the stigma of an individual flower: these figures give the daily rate of presentation of new flowers.

	Doronicum caucasicum	*Anthemis montana*	*Eupatorium raffillii*
Day 1	5 flowers open	6 flowers open	8 flowers open
,, 2	+30 ,, ,,	+14 ,, ,,	+10 ,, ,,
,, 3	+15 ,, ,,	+12 ,, ,,	+ 8 ,, ,,
,, 4	+25 ,, ,,	+19 ,, ,,	+14 ,, ,,
,, 5	+30 ,, ,,	+17 ,, ,,	+11 ,, ,,
,, 6	+10 ,, ,,	+10 ,, ,,	+10 ,, ,,
,, 7	+11 ,, ,,	+14 ,, ,,	+ 7 ,, ,,
,, 8	+11 ,, ,,	+16 ,, ,,	+ 6 ,, ,,
,, 9	+15 ,, ,,	+11 ,, ,,	+ 8 ,, ,,
,, 10	+26 ,, ,,	+ 2 ,, ,,	+ 8 ,, ,,
,, 11	+10 ,, ,,	+16 ,, ,,	+ 5 ,, ,,
,, 12	+10 ,, ,,	+18 ,, ,,	+ 4 ,, ,,
,, 13		+ 7 ,, ,,	
,, 14		+ 8 ,, ,,	
,, 15		+10 ,, ,,	
,, 16		+10 ,, ,,	
,, 17		+ 5 ,, ,,	
,, 18		+ 8 ,, ,,	
,, 19		+ 4 ,, ,,	

If *Anthemis montana* were self-incompatible (it is not recorded by Fryxell) there would be 19 separate days on which cross-pollination could take place. If one makes an absurd simplification and imagines that all the flowers newly opened on each day are pollinated by a single pollen-laden insect, and that, the population being reasonably large, this insect comes daily from a different plant: then 19 inter-plant hybridizations will result in one capitulum. In practice multiple pollinators, proximity-effects, the production of several flowering capitula by one plant and mixtures of pollen on visiting insects are some of the factors which will combine to complicate the results. Practical investigation needs a plant with a number of strains (easily recognisable in F_1) well in excess of the number of days over which a capitulum remains in flower.

THE CONTRAST OF CAPITULUM AND SINGLE FLOWER.

The duration of individual flowers in such polypetalous genera as *Ranunculus, Anemone, Paeonia, Meconopsis, Magnolia* was found to be about a week (4-10 days); the periods of stigmatic receptivity have not yet been recorded, but will certainly be shorter than this.

Good (1931; 1956, p. 322) has attempted to make an economic comparison between the single flower of *Anemone* and the capitulum of *Cosmos*; his inability to show that the latter is more efficient is a factor in his scepticism about evolutionary progress. Van der Pijl (1958) correctly points out that such a comparison

s as inappropriate as one in the range fish-mammal-whale: as he says, "*Anemone* is a specialised Ranalian, an early parallel of, not a precursor of *Cosmos*". The other answer to the question is this: *Anemone* is a specialised member of Ranunculaceae and the success of its flower-type is measured by some 120 species; *Cosmos* is a member of Compositae, the success of whose flower type is measured by some 18,000 species. Not the least important difference may be that the composite capitulum presents possibilities for a vastly increased range of cross-pollination, with subsequent genetic recombination.

We do not know how many pollen-parents may be represented in the seed-production of a single flower of *Anemone*. The serial maturation of the stigmas is more rapid than in a composite lead and the spatial separation is less. One might thus expect rather fewer males to be involved in the seed production of an *Anemone* flower than in a composite head of comparable size.

It is beyond dispute that capitular inflorescences, especially the patterns found in Compositae, have achieved considerable biological success measured in number of species*. In contrast to this the other highly successful floral type is the single flower with zygomorphic corolla, specialised pollination mechanism and an ovary containing very numerous ovules. Such flowers are characteristic of *Orchidaceae, Scrophulariaceae* and its close allies (*Gesneriaceae, Orobanchaceae, Bignoniaceae*), etc. This arrangement might seem to be the antithesis of that in Compositae, but it may simply represent a different means of achieving a high rate of genetic recombination. In these elaborate single flowers a very large number of ovules are fertilised by pollen from one, or a few, male parents. This will lead in due course to *intensive* exploration of the possible recombinations between the plants that cross. In Compositae, where individual ovules are individually pollinated (neighbouring ones often receiving pollen from different plants) the exploration of possible recombinations is *extensive* through the population rather than *intensive* between individual plants.

A flower with a single stigma may receive mixed pollen, either from a pollinator which has previously visited several other plants

*Another dominant group showing the one-stigma/one-ovule relationship is, of course, Gramineae. As grasses are wind-pollinated the diffuse panicle is a far more efficient type of inflorescence than a capitulum would be and predominates in the family.

or from a succession of pollinators. In the latter case a determining factor will be the duration of stigmatic receptivity. In many plants with large zygomorphic flowers it is known to be short, and in certain orchids (e.g. *Cymbidium, Odontoglossum*) the flowers wither within a few hours of pollination, although if unpollinated they remain fresh for many days. The whole subject of effective duration of various phases of the flower needs a critical summary.

REDUCTION AND SECONDARY AGGREGATIONS OF CAPITULA.

The second part of the problem of Compositae lies in the apparent trend, within the family, from the solitary many-flowered head to few-flowered or single-flowered heads congested into secondary capitula. Explanations, or descriptions, have been given in various terms; Cronquist (1951, 1956) offers an orthogenetic interpretation, saying, in effect, that there is an inherent tendency in the family to vary in this direction and formulating a genetic mechanism to permit it; Good (1956, p. 309) speaks of 'pseudanthia of pseudanthia' without attempting an explanation of their occurrence, clearly because he believes evolutionary developments are not necessarily subject to causal explanations (1956, p. 387-388); Corner's description of the capitulum in terms of the transference of function can be repeated at a secondary level, for the compound capitulum; Melville (1957, p. 298) has accepted Turing's reaction-diffusion theory of morphogenesis and regards the production of capitula of capitula as the building of structures developed in the previous evolutionary cycle into new aggregations, due to the repetition of the "existing and ancestral wave-patterns inherent in the genetical make-up of the organism". Repetitive evolutionary cycles are also implicit in the remarks of Danser (1950, p. 158), van der Pijl (1958, p. 36) and Leppik (1960); all these ideas being somewhat cognate to Gaussen's concept of pseudocyclic evolution (or surévolution), on which I will quote an explanatory footnote from a recent paper on Araucariaceae (Gaussen, 1957, p. 253): "Je rappelle que cette conception admet dans chaque pseudocycle: un type compliqué: *primitif*; l'évolution se fait vers un type plus simple et specialisé: c'est le type évolué; le pseudocycle se termine par la soudure des types évoloués ou des multiplications diverses qui donne le type *surévoloué* qui resemble plus ou moins au type primitif. Ce type

surévoloué sert de type primitif à un nouveau cycle sauf dans le cas de sénilité".

No biologist who has the living plants themselves in the forefront of his mind will find any of these approaches very illuminating. What facts are there available?

In the first place is there any indication of repeated mutations in the same direction, towards smaller capitula? Cronquist (1955, p. 494) admits that there may be exceptions to the general trend. There are many genera in which species having the largest capitula also have specialized features, suggesting that large capitula are derived, not primitive, for the genus. To name a few: *Carlina* (*C. acaulis* is an acaulescent alpine), *Vernonia* (*V. primulina,* a species with thick, almost fleshy, rhizomes found in grasslands liable to burning), *Erigeron* (*E. glaucus,* a fleshy-leaved maritime species), *Inula* (the large-leaved *I. helenium* and *I. royleana*), *Tragopogon* (see Stebbins, 1950, p. 495), *Venidium* (*V. wyleyi,* an annual): there are many others.

Furthermore, in every genus that has been grown commercially, selection for larger flower heads has proved a simple matter. *Aster, Calendula, Callistephus, Dahlia, Chrysanthemum, Helianthus, Bellis, Tagetes, Zinnia* and so on; they all illustrate this point.

Dr. Stebbins has suggested to me that the emphasis laid on the trends towards reduction may well owe much to reduction being more easily observed than increase. It is certain that generic descriptions very frequently give the lower limit of the number of flowers in the capitulum, seldom the upper. There is very little actual numerical data about flower heads containing more than thirty flowers.

In some groups and genera reduction series undoubtedly exist, in others the capitula showing the largest capitula are derived. There is no reason to suppose that, in the family as a whole, the genetic variation in the size of the capitulum shows a distribution constantly biassed in one direction. Larger capitula, because they are more conspicuous and produce more seed, will carry a natural advantage unless, or until, they are exposed to selection pressures which can be evaded by a decrease in size.

The evolution of secondary capitula of 1- or few-flowered heads is not a single problem. Just as there are different types of capitula, so also of compound capitula. There is little in com-

mon between *Sphaeranthus* and *Echinops* and they can only be given a superficial unity by such philosophical theories as cyclic evolution or orthogenesis. Nor does reduction in the number of flowers in the head necessarily lead to secondary capitula (as it should were 'cyclic' phenomena involved). Many species of *Vernonia, Staehelina uniflora,* and the whole genus *Corymbium,* are characterized by spreading corymbs of one-flowered heads; and corymbs of few-flowered heads (*Erlangea, Achillea, Lactuca,* etc.) are much commoner than secondary capitula.

Few-flowered heads may occur in other arrangements; erect in a spaced panicle (*Cacalia uniflora*) or pendulous (*Prenanthes purpurea*). Each instance is an individual problem. Nevertheless there are one or two general factors which could be important in determining reduction trends; four of these, duration of flowering, sex-ratios, insect attack and mechanical strength will now be briefly examined.

A compound capitulum of *Echinops,* consisting of about 200 1-flowered primary capitula, has a duration of about three weeks. This shows no marked extension over a simple capitulum of the same size. More detailed records for compound capitula have not yet been made, but the following data for a cyme of 9 small capitula of *Olearia mollis* suggest that the duration is somewhat extended relative to the total number of flowers:

No. of rays	No. of disc fls.	Duration
8	5	31 May-11 June
8	7	1-11 June
10	6	2-12 ,,
10	9	3-14 ,,
8	9	4-15 ,,
11	8	5-15 ,,
11	9	6-18 ,,
9	10	8-19 ,,
10	6	18-25 ,,
Totals: 85	69	31 May-25 June=26 days

One effect of more numerous but smaller heads in a plant of the *Callistephus* type (with peripheral female flowers and central hermaphrodite ones) will be that the ratio between the two sexual types will tend to be equalised by a relative increase in the number of rays. This is well shown in the data for *Olearia mollis* just given. Such a change will increase outbreeding. A flexible balance between inbreeding and outbreeding may be important at certain stages of evolution. The difference between *Erigeron*

and *Aster* (very numerous narrow rays compared with fewer broader ones) could reflect another way in which this balance can be varied.

Anyone who has collected thistle seeds is familiar with the experience of pulling out a head-ful of pappus and finding underneath nothing but a mass of insect frass. Smaller capitula, even if closely aggregated, will afford a measure of protection against insect damage by containing the enemy to a smaller foraging area. Cameron (1935) records that the larva of *Pegohylemyia seneciella* consumes 75% of the ovaries in the head of *Senecio jacobaea* in which it is hatched and may, in some areas, infect a third of the heads; the attacks of the knapweed gall-fly (Varley, 1947; Wadsworth, 1914) cause considerable loss of seed in *Centaurea nigra*; the activities of a fly, *Acanthiophilus helianthi,* virtually eliminated the cultivation of saff-flower (*Carthamus tinctorius*) from France (cf. Knowles, 1955) and the sunflower moth (*Homoeosema electellum*) it is a potent factor in sunflower cultivation. In some sunflowers (*Helianthus*) and other Compositae protection against insect attack is given in another way, by the development of a carbonaceous layer in the seed coat (Hanausek, 1902 and 1920; Vavilov, 1951, p. 150). It is clear that the consumption of seeds by insects eliminates many of the progeny: anything which lessens this loss is likely to be selected and perpetuated.

Finally, mechanical considerations suggest that a corymb of small capitula, as is found in *Achillea millefolium* or *Vernonia uniflora,* is a far sounder structural unit than a single large capitulum containing the same number of flowers. The single unbranched peduncle topped by a large head is very vulnerable. By comparison the many-strutted corymb is not merely stronger overall: damage to a few lateral struts will leave the remainder of the corymb unaffected.

The points just mentioned do not fully explain the evolution of secondary inflorescences of few-flowered capitula in Compositae. They suffice to suggest that the problem is open to practical investigation.

THE FATE OF THE PAPPUS.

Wind-dispersal of the fruits is, in common opinion, a characteristic feature of Compositae. Yet the pappus is often absent, or functionless in dispersal.

Vernonia is a large tropical genus of some 800 species and has a setose pappus. Closely related is the African *Erlangea* in which the pappus is caducous before the fruits ripen; there are some 30 species. *Ethulia conyzoides* is a widespread tropical weed in which the pappus is completely absent. In the last two genera the involucre appears to close over the fruits when damp and to open when dry, so that the fruits may be shaken out as from a censer. The absence of pappus marks other widespread weeds: *Matricaria matricarioides, Bellis perennis, Lapsana communis.*

In *Bidens* and *Coreopsis* the pappus consists of a few rigid and barbed aristae, which aid the dispersal of the fruits by adhering to the coats of passing animals. Often animal-dispersal is achieved by hooks on the involucre, in which case the fruiting head is moved. In some (*Arctium*) the individual fruits are eventually set free, in others (*Xanthium*) the few fruits in the head remain held together. This also occurs, not associated with animal dispersal, in certain Compositae of arid areas, for instance *Gorteria* (Hutchison, 1918) and *Cuspidia* (Burtt, 1948) in South Africa, *Erodiophyllum* in West Australia. This retention of the fruits within the head (synaptospermy: Murbeck 1920, 1943; cf. p. 218 above) may be a further factor in favouring a relatively small number of flowers in the head: no large capitula behave in this way, but in *Didelta* (Burtt, 1948) the capitula (of about 35 fertile flowers) break up into three synaptospermous segments, suggesting that there is a maximum size above which this system is uneconomical. It is, however, an evolutionary cul-de-sac and does not lead to secondary aggregations of capitula, because the few-seeded disseminule is the efficient functional type.

In many Compositae there is a difference in the development of the pappus between outer and inner flowers. This may be associated with differences in the flowers themselves: for example in *Galinsoga parviflora* the female ray-flowers are epappose whereas those of the disc are pappose (see illustration in Ross-Craig, 1960, pl. 27; but cf. *G. ciliata,* pl. 28, where the pappus is developed on both types of flower). In ragwort (*Senecio jacobaea*) the pappus acts as the dispersal mechanism for the central fruits of the capitulum, but is caducous from the marginal ones (derived from ray flowers?) which remain pressed against the inside of the involucre and are therefore not dispersed far from the parent plant (Green, 1937).

In *Lapsaneae,* where all the flowers are ligulate, Zohary (1950) has traced a reduction series not only from genus to genus, but within individual heads. In *Hedypnois cretica* the setose part of the double pappus is entirely missing on the marginal flowers, but is present on the central ones, and intermediate stages occur in between. Zohary says "the reduction of the pappus has taken place in a centrifugal direction", but this expression needs revision in terms of the ontogeny of the flower-head. As the capitulum is a racemose structure with the youngest flower at the centre, it seems right to regard the pappus as gradually coming into development. It can then be seen that the absence of the pappus from marginal flowers would be brought about if a mutation arose which simply delayed the expression of pappus-formation. Combined genetic and morphogenetic investigation might well be possible.

The wind-borne pappose fruit is a better agent for widespread dispersal than it is for accurate ecological distribution. The absence of pappus in many weeds may indicate that transport in mud on the hooves of passing animals, and subsequent colonization of the disturbed ground at the side of animal trackways, drinking places and so on, is more efficient than widespread random dispersal. Such plants would prove admirably preadapted for the coming of man with his wheeled transport. *Ethulia, Lapsana, Bellis* and *Matricaria matricarioides,* mentioned above, are examples.

The pappus or involucre that clings to animal-fur may similarly increase the ecological accuracy of dispersal. Dissemination of propagules by animals is regarded by Stebbins (1949, p. 240) as the third and highest level in his hierarchy of reproduction.

Loss of pappus is often a specialization in the dispersal arrangements of Compositae and is not to be regarded as a retrograde loss of the efficient mechanism for widespread wind-borne dispersal. The pappus has almost certainly played an important part in achieving the vast distribution of the family, but in any particular group under particular conditions there is no reason to suppose that specialization towards more precise means would not be advantageous.

CONCLUSIONS: THEORETICAL.

It is dangerous to assume that the capitulum is merely to be regarded as a second-order flower. In its biological organization (numerous single-seeded flowers opening in extended succession) the segregation of the ovules is as important as the aggregation of the flowers. The result is a breeding pattern which is not that of any individual flower and may represent a highly efficient system for the exploration of genetic recombinations. The single flowers in some specialized families (Orchidaceae is the best example) may be equally efficient in a different way, attaining their exploration of the available genetic material by the fertilization of a very large number of ovules by pollen from a single male parent. In Compositae the floral organisation may be termed collectivist and the genetic exploration is extensive: in Orchidaceae the flowers may be termed individualist and the genetic exploration is intensive.

Compositae are essentially plants of open country, not highly specialised to particular pollinators, usually occurring in fair numbers. Orchidaceae are essentially plants of tropical forests, highly adapted to specific pollinators, often occurring in scattered populations. Compositae demand numerous insect-visits, so that the isolated act of pollination is a commonplace: in orchids a single pollination is an important event.

Behind these two families as leaders, two teams of other families can be marshalled: these show the same general tendencies, though often to a less degree. In the collectivist team, for example, are Calycereae, Dipsacaceae, Eriocaulonaceae: amongst the individualists Gesneriaceae, Bignoniaceae, Asclepiadaceae. One may reconsider other families with the same ideas in mind, even if they do not wholly conform to the collectivist-individualist pattern. For instance, Leguminosae (cf. *Lathyrus odoratus* and *Trifolium*) and Rubiaceae (cf. *Randia* with *Galium* or *Sarcocephalus*) seem to show that both trends may develop within one family. The theme requires extension and critical investigation.

It is artificial classification to unify the manifold examples of reduction in capitulum-size into a general trend. At least, if that is done, it must be recognized as a device descriptive merely of the results of a variety of causes working in a variety of circumstances. It is wholly inadmissible to proceed to an

Vernonia stenostegia (Stapf) Hutch. & J. M. Dalz. Native of Nigeria. Flowers all hermaphrodite, number (in 4 heads) varying from 139-153. First flowers standing erect on day of opening, subsequently bending over outwards and later flowers following same behaviour. Period of opening: 8-10 days under greenhouse conditions. Plant apparently self-incompatible: achenes developed, but all empty. Note that the open flowers do not at any time form a flat-topped disc. Flower-colour: light pinkish-purple (cf. *Bot. Mag.*, t. 8981: 1923).

argument that the trend, because it is widespread through the family, must be inherent and must be controlled by orthogenetic mutation. The table of primitive and advanced characters given by Cronquist (1951) may well be valid in terms of morphological change, but they provide no basis for orthogenetic theory: a degree of unity in morphology may stem from many different causes.

Allied plants are known to show similar genetic variations and, because the range of variation is always limited, *similar* variants may become established and perpetuated by *similar or different* selection-pressures, or merely by being linked to some other varying and more vital character. Change being of nature's order, we must expect, in any family, both divergence and convergence. We presume too far on our ignorance if we say that the manifold divergences cannot be advantageous or that the convergences are inexplicable in practical terms. Each is a necessary feature of a large and diversified family, and we have no sure evidence yet that normal variation, selection, fortuitous linkage to other selected characters and other known mechanisms of evolution (cf. Stebbins, 1950) fail to account for the results we see. What we have to do is to collect and investigate all the available data and test it against our current knowledge of ways and means.

CONCLUSIONS: PRACTICAL.

The family deserves more critical investigation than it has yet received. A classification of capitulum-types is one requisite, and a photographic record, combined with notes on the distribution of the sexes and the fertility system of the plants, would be a great help in forming this (cf. plate V). The whole interlocking of morphology and breeding system needs careful study. Harland (1955, p. 18) has pointed out that discoid groundsels such as *Senecio vulgaris* are self-compatible, while radiate species like *S. squalidus* are self-incompatible; Clausen, Keck and Hiesey (1945) record that the long-rayed species of *Madia* are self-incompatible, the short-rayed species self-compatible; the possible effects of size of head and width of rays on the percentage of outbreeding has been mentioned already (p. 224). It is certain that the morphological evolution of Compositae has not proceeded in disregard of changes in, and demands upon, the breeding system.

Similarly the capitulum as inflorescence interlocks with the capitulum as infructescence. These interactions are almost virgin territory for the investigator.

Many botanists must have notes relevant to the biology of this huge family and there must be much valuable data buried in the literature. The assembly of all this material is more than one man's work and I am therefore prepared to file and index any data and references sent to me at the Royal Botanic Garden, Edinburgh, and to keep it available for consultation by visiting botanists. If the response to this suggestion justifies them, interim reports and summaries may be published.

I am indebted to a number of botanical friends for discussions on the topics touched upon in this paper, and particularly to Dr. G. L. Stebbins who read a draft and made some very useful criticisms. Observations on living plants at Edinburgh, of which only a few are quoted, were made for me by Mr. P. J. B. Woods, and I am grateful for his care in this tedious work.

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NOTES ON THE SCOTTISH FLORA.

Mountain Plants in Peeblesshire (v.c. 78) and Selkirkshire (v.c. 79).

A recent account (Ratcliffe, in *Trans. Bot. Soc. Edinb.*, **37**, 251-271: 1959) of the mountain plants of the Moffat Hills was concerned mainly with the richer part of this area, in Dumfriesshire. Since then, several of the rarer Moffat plants have been found in the Peeblesshire and Selkirkshire catchments and these are here placed on record. Crags are few and small beyond Moffat Water itself, and the species in question are mostly those of acidic heaths or calcareous flushes on the upper slopes of the gently contoured Broad Law (2,754 ft.), Cramalt Craig (2,723 ft.), and Dollar Law (2,680 ft.).

On 4th October 1959, *Chamaepericlymenum suecicum* was seen in fair quantity in its old Peeblesshire locality on Dollar Law, growing mainly in *Vaccinium myrtillus* and *Nardus stricta* snow-bed communities on the north and east slopes at over 2,000 ft. Crossing over into Selkirkshire I found this species growing very sparingly in an extensive bed of *Vaccinium myrtillus* at 2,300-2,500 ft. on the steep north-east slope of Cramalt Craig. On the same slope were a good many springs, mostly dominated by bryophytes such as *Aplozia cordifolia*. The spring water gives extensive irrigation to the adjoining ground, as shown by the mixture of moderately calcareous flushes, flush bogs and grasslands, with their characteristic complement of basiphilous herbs, grasses and bryophytes. The springs, flushes and rills produced *Epilobium anagallidifolium, E. alsinifolium, Sedum villosum, Veronica serpyllifolia* ssp. *humifusa, Saxifraga stellaris* and *Cochlearia alpina,* while *Thalictrum alpinum* and *Saxifraga hypnoides* belonged more to the adjoining communities.

A return visit was paid to this locality on 19th June 1960, when I found a single flowering plant of *Alopecurus alpinus* growing in one of the bryophyte springs. The habitat agreed very closely with that mentioned (*op. cit.*) for this plant on the White Coomb about six miles away. An unusual-looking *Myosotis* collected in this series of springs and in a smaller system of rills at about 1,700 ft. on the east slope of Dollar Law (v.c. 78) was identified by Mr. A. E. Wade as *M. brevifolia*. The plant was

quite plentiful within its habitat in both localities. *Myosotis brevifolia* was recorded many years ago from the Moffat Hills in Dumfriesshire but does not seem to have been noticed elsewhere in Scotland.

The more notable bryophytes found on the Cramalt Craig were *Splachnum vasculosum, Hypnum callichroum, Hylocomium umbratum, Meesia uliginosa, Bryum weigelii* and *Sphagnum warnstorfianum.*

Another series of calcareous flushes in the north corrie of Broad Law (v.c. 78) was examined on 11th October 1959 and yielded *Sedum villosum, Saxifraga hypnoides, S. stellaris, Cochlearia alpina, Meesia uliginosa,* and a *Myosotis* which again appeared to be *M. brevifolia,* though this was not confirmed. The broken rocks above were interesting mainly for their bryophytes, *Dicranum falcatum, Arctoa fulvella, Oedipodium griffithianum, Grimmia torquata, Gymnomitrium concinnatum* and *Radula lindbergiana* being found there.

Calcareous rocks outcrop fairly extensively around the head of Talla Reservoir in the same area of Peeblesshire, but at rather a low elevation, and mountain plants are few in number. *Saxifraga hypnoides, Cochlearia alpina* and *Oxyria digyna* occur plentifully, as do ascending lowland species such as *Helictotrichon pratense* and *Arabis hirsuta. Orthilia secunda* (*Pyrola secunda*) grows sparingly on the Garelet Hill and *Vicia sylvatica* in the ravines of Cairn Law.

Carex bigelowii is abundant locally in the *Rhacomitrium* heaths of the high watershed between Broad Law and Dollar Law, but *Salix herbacea* has been noticed only on rocks on the Selkirk side of Cramalt Craig. The blanket-bogs of these hills usually contain a profusion of *Rubus chamaemorus,* which is perhaps the most distinctive and widespread mountain plant in the eastern half of the Southern Uplands.

As a final note, a new locality for *Arctostaphylos uva-ursi* was found in the Moffat Hills in May 1960, so that the species is not yet extinct in Dumfriesshire. Several flourishing patches of this plant, at least one in flower, were seen on a dry, acidic crag in the valley of the Tail Burn.

DEREK A. RATCLIFFE.

Further Additions to the Flora of Foula.

In 1956 and 1957 K. Guy Messenger and J. Gordon Urquhart made collections of the flora of this island, the results of which were published in *Trans. Bot. Soc. Edinb.*, **37**, 278 (1959). Since then, in 1959 and 1960, I have collected several specimens hitherto not recorded in the Foula flora, as follows:—

Selaginella selaginoides (L.) Link. Most parts of island. (Recorded by Turrill (*Rept. Bot. Exch. Club*, **8**, 838: 1929) but not confirmed by Messenger or Urquhart.)

Asplenium marinum L. On cliffs from Sneck to Wester Hoevdi, and Back of Noup.

Ranunculus ficaria L. Ham Voe and North Bay under boulders.

Capsella bursa-pastoris (L.) Medic. Ham garden.

Hypericum pulchrum L. Above Blobersburn.

Sagina nodosa (L.) Fenzl. Springs, Loch and North End.

Lathyrus pratensis L. Gravins.

Ligusticum scoticum L. Near top of cliffs from Soberlie to Kame. Stack of the Gaads.

Polygonum viviparum L. Common on top of Sneug, and Hamnafjeld. (Found by Lewis (*Trans. Roy. Soc. Edinb.*, **47**, 795: 1911) but not confirmed by Turrill or Messenger and Urquhart.)

Rumex longifolius DC. Common in kailyards and beside burns and ditches. (Recorded by Turrill but not confirmed by Messenger or Urquhart.)

Rumex obtusifolius L. Common in kailyards, ruins, etc.

Vaccinium uliginosum L. Hamnafjeld and Sneug.

Anagallis tenella (L.) L. Wet ground at North End.

Littorella uniflora (L.) Aschers. Very common in peat bogs, ditches and edges of pools. (Recorded by Turrill but not confirmed by Messenger or Urquhart.)

Antennaria dioica (L.) Gaertn. Only a few plants near top of Hamnafjeld.

Matricaria matricarioides (Less.) Porter. Few plants growing on Ham path.

Taraxacum officinale Weber. Ham garden. Brought in accidently among flower roots.

Taraxacum sp. (aff. *T. spectabile* Dahlst.) Under boulders of North Bay.

Listera cordata (L.) R. Br. Moorland.

Coeloglossum viride (L.) Hartm. (*Habenaria viridis* (L.) R. Br.). Along South Banks and South Ness.

Festuca vivipara (L.) Sm. Generally distributed on the hills and the lower moorland. Recorded by Lewis as *Festuca ovina* var. *vivipara,* but not confirmed by Turrill or Messenger and Urquhart, unless this is Turrill's "*Festuca rubra* (viviparous)".

There are also various plants which have been introduced. The trees all come from sheltered positions in gardens and kailyards. The "plantation" planted by my grandfather at the beginning of this century and mentioned by Lewis (*l.c.,* p. 806) has completely disappeared, due to sheep and rabbits more than exposure.

Acer pseudo-platanus L. Ham kailyard.

Rubus idaeus L. Old Leiraback byre.

Rosa rugosa Thunb. Bight of Ham burn, introduced from Tresta, on the Shetland mainland about 50 years ago.

Sorbus aucuparia L. Old Leiraback byre beside burn.

Salix alba L. Ham kailyard.

Salix phylicifolia L. Bight of Ham burn, introduced with the *Rosa rugosa.*

Sambucus nigra L. Kailyards and gardens.

Chrysanthemum vulgare (L) Bernh. (*Tanacetum vulgare* L.). Mucklegrind, behind Ham.

Phleum pratense L. Among cut hay behind Haa. Sown from seed but did not survive the 1960 winter.

The specimens upon which these records are based have been deposited in the Herbarium at the Royal Botanic Garden, Edinburgh, where their determinations were confirmed by Mr. P. S. Green.

SHEILA C. HOLBOURN.

NOTES ON THE LICHEN FLORA OF FAIR ISLE, SHETLAND (v.c. 112).

During May and June 1954 I visited Fair Isle and made a small collection of lichens. The notes which follow are based on my records during this visit, and make no pretence of being a complete list. A map of Fair Isle was published by Pritchard (in *Proc. B.S.B.I.,* **2**, Pt. 3: 1957), and most of my localities are

shown there. My grateful thanks are due to Dr. D. N. McVean for assisting me with determinations, and the nomenclature and order is that of Watson (*Census Catalogue of British Lichens*: Brit. Mycol. Soc., 1953).

LIST OF LICHENS.

6/77 *Parmelia saxatilis* (L.) Ach. Cliffs W. of Ward Hill (500 ft.) and cliffs at North Haven (20 ft.).

6/78 *P. omphalodes* (L.) Ach. Cliffs at North Haven (120 ft.).

7/87 *Hypogymnia physodes* (L.) Wats. Summit of Ward Hill (700 ft.).

25/546 *Ramalina scopulorum* (Retz.) Ach. Widespread on cliffs and wall-tops.

25/548 *R. curnowii* Cromb. Dyke on Burrashield. New vice-county record.

32/613 *Icmadophila ericetorum* (L.) Zahlbr. Peaty soil in the Gully, spreading to adjoining rocks. Similar habitats near the N. Light. Common.

40/697 *Xanthoria parietina* (L.) Th. Fr. Abundant on cliffs and walls all round the island, especially in the west, where some cliffs are a spectacle of orange colour.

47/753 *Pseudophyscia fusca* (Huds.) Wats. Cliff tops at Malcolm's Head (200 ft.) and at N. Light (200 ft.). Also on dykes on Burrashield (400 ft.).

60/881 *Cladonia uncialis* (L.) Web. Bare, peaty places among stones, on Ward Hill (500 ft.).

60/885 *C. foliacea* (Huds.) Schaer. Cliffs near N. Light (200 ft.).

60/889 *C. pyxidata* (L.) Hoffm. Moorland near the croft of Stoneybrake (200 ft.).

60/897 *C. cervicornis* (Ach.) Schaer. var. *subcervicornis* Wain. The Gully (120 ft.).

75/990 *Lobaria laetevirens* (Leight.) Zahlbr. Cliff around N. Haven (80 ft.). New vice-county record.

77/994 *Peltigera canina* (L.) Willd. Occurring among heather on summit of Ward Hill, and on wet moorland on lower slopes. Also in the Gully (120-700 ft.).

77/999 *P. polydactyla* (Neck.) Hoffm. Rocks in the Gully (120 ft.).

87/— *Collema* Sp. Overhanging banks of stream, Vaadal (150 ft.).

132/1254 *Sphaerophorus fragilis* (L.) Pers. Soil in Vaadal (200 ft.).

A. Currie.

Pyrola chlorantha—A Scottish Species?

The above heading was used for an exhibit shown at the C.S.S.F. meeting held in Glasgow on 12th November 1960 (see p. 243). It therefore seems necessary either to falsify the report by expunging it from the list, or to publish a few words of explanation. The latter course is, rather hesitatingly, adopted.

Pyrola chlorantha Swartz is not a British species, but is found both in Scandinavia and in Central and Western Europe. During a visit to Edinburgh, Dr. G. Knaben, of the University of Oslo, examined the material of *Pyrola* in the Royal Botanic Garden herbarium and pointed out that one sheet contained *Pyrola chlorantha* mixed with *P. media*. The label on the sheet in question showed that it had already been separated from a specimen of *P. rotundifolia* before mounting. The collector was given as J. Mackay (1772-1802) and the locality as Bengloe (Perthshire): the specimen had come to Edinburgh as part of the herbarium of the Brodie of Brodie, but had apparently not been mounted till about 1910: there was, therefore, ample time for some mixture to have occurred. On the other hand, Ben-y-gloe has not been over-explored botanically, *Pyrola* species are easily confused and no specimen has been found in the European covers from which these plants of *P. chlorantha* seem to have been separated. There is, therefore, an outside chance that *P. chlorantha* is a Scottish plant. Anyone in the Ben-y-gloe area should keep a sharp look-out for it.

P. chlorantha has the curved style of *P. rotundifolia* but differs from that species in having yellowish-green flowers in short racemes, shorter oval-triangular (rather than lanceolate-acute) calyx lobes and much smaller almost entire leaves. I take these characters from Coste, Flore de France: they seem applicable to the specimen concerned.

B. L. Burtt.

Report of the Alpine Section, 1960.

By J. Grant Roger.

Meeting centred at Garth Memorial Hostel, Perthshire.
(18th and 19th June, 1960.)

On 18th June a party of 11 visited Glen Loch in Atholl, mainly with the object of exploring the calcareous schists immediately east of Loch Loch. The journey up Gleann Fearnach was made by car (with permission) over the estate road to Doldhu then by foot along the track running northward on the east side of Glen Loch.

Outcrops of calcareous rock were first encountered at an elevation of about 1700 ft., $\frac{1}{4}$ mile south of the Loch, where *Arabis hirsuta, Carex capillaris, C. pulicaris, Helianthemum vulgare, Juncus triglumis, Linum catharticum, Mercurialis perennis, Polygonum viviparum, Saxifraga aizoides, S. oppositifolia, Thymus drucei* and *Tofieldia pusilla* were found. On the adjoining moorland *Calluna vulgaris* and *Vaccinum myrtillus* were abundant while *Alchemilla alpina, Anthoxanthum odoratum, Carex pilulifera, Nardus stricta, Pinguicula vulgaris, Polygala serpyllifolia, Potentilla erecta, Rubus chamaemorus* and *Vaccinium vitis-idaea* were present. A few plants of *Listera cordata* occurred very locally in damp places sheltered by the *Calluna*.

Much time was spent exploring the steeper crags overlooking Loch Loch and on these the following species of vascular plants in addition to those mentioned above were noted, chiefly between 1700 and 1850 ft.:—*Alchemilla glabra, Asplenium ruta-muraria, A. trichomanes, A. viride, Botrychium lunaria, Chamaenerion angustifolium, Cystopteris fragilis, Draba incana, Galium boreale, G. pumilum, Geranium sylvaticum, Geum rivale, Helictotrichon pratense, Luzula sylvatica, L. spicata, Oxytropis campestris, Polypodium vulgare, Polystichum lonchitis, Potentilla crantzii, Rubus idaeus, Solidago virgaurea, Sorbus aucuparia, Thelypteris phegopteris* and *Veronica fruticans*. Among the mosses characteristic of the crags were *Cratoneuron commutatum, Ctenidium molluscum, Distichium capillaceum, Fissidens cristatus, Grimmia funalis, Gymnostomum aeruginosum* and *Plagiopus oederi*.

The flora of the grassy slopes at c. 1800 ft. included: *Alchemilla alpina, Anthoxanthum odoratum, Antennaria dioica,*

Briza media, Calluna vulgaris (local), *Campanula rotundifolia, Festuca ovina, Fragaria vesca, Galium verum, Nardus stricta, Oxalis acetosella, Polygala serpyllifolia, Polygonum viviparum, Silene dioica, Thymus drucei, Vaccinium myrtillus, V. vitis-idaea* and *Viola lutea.*

Time did not permit a thorough exploration of this very interesting, but rather remote, area of calciferous schistose crags, nearly all well below 2000 ft. in elevation yet supporting a flora remarkably rich in montane species, the most noteworthy of these being *Oxytropis campestris* (first found here by J. Ferguson in 1887).

On 19th June the party climbed Cairn Gorm (3370 ft.), north side of Glen Lyon, ascending by the path from Invervar and approaching the mountain from the east. We explored the rocks of calcareous schists chiefly between 2000 ft. and 2500 ft., noting there fine plants of the following species: *Carex rupestris, Draba incana, Dryas octopetala, Juncus triglumis, Oxyria digyna, Potentilla crantzii, Salix arbuscula, S. myrsinites, S. reticulata, Saussurea alpina, Saxifraga aizoides, S. hypnoides, S. nivalis, S. oppositifolia, S. stellaris, Thalictrum alpinum* and *Tofieldia pusilla.* The very handsome calciphilous moss *Orthothecium rufescens* was prominent locally.

On the slopes immediately beyond the crags the vegetation consists largely of *Alchemilla alpina, Anthoxanthum odoratum, Blechnum spicant, Carex pilulifera, Deschampsia flexuosa, Festuca ovina, Nardus stricta, Vaccinium myrtillus* and *V. vitis-idaea.* In some of the stony flushes *Armeria maritima, Carex saxatilis* and *Triglochin palustris* occurred.

From about 2800 ft. upwards the vegetation of the acid heathland (on quartzite) includes *Alchemilla alpina, Carex rigida, Galium saxatile, Nardus stricta, Salix herbacea* and *Vaccinium myrtillus.*

The descent of Cairn Gorm was made eastwards by the head stream of the Invervar Burn and by way of the southern slopes of Meall Garbh (3150 ft.) where on a small area of rather steep schistose rocks, at about 2500 ft., we found a few plants of *Erigeron borealis* associated with *Angelica sylvestris, Botrychium lunaria, Carex atrata, C. vaginata, Draba incana, Luzula sylvatica, Potentilla crantzii, Saxifraga hypnoides, S. oppositifolia, Sedum rosea, Silene acaulis* and *Trollius europaeus.*

Committee for the Study of the Scottish Flora.

Sixth Annual Report to 31st December 1960.

The Committee has met three times (at Glasgow in March and November and in Edinburgh in October), has held three Exhibition Meetings (at Queen's College, Dundee, by permission of Dr. Edith Smith, on 19th March; at the Academy, Elgin, by permission of the Rector, on 20th March, and at the University of Glasgow, Department of Botany, by permission of Professor J. Walton, on 12th November), and six Field Meetings (at Elgin, 10th-13th June, led by Mr. J. G. Roger; at Garth Field Studies Centre, Perthshire, 17th-19th June, led by Dr. D. Ratcliffe; at St. Cyrus, 8th-11th July, led by Dr. C. H. Gimingham; at Duns, 30th July-6th August, led by Dr. F. H. Perring; in the Shetland Isles, 6th-20th August, led by Mr. R. Palmer and the Chairman, and at Garth Field Centre (Cryptogamic Foray), 17th-19th September, led by Mr. D. M. Henderson). The Committee also made arrangements for the first meeting of the members of B.S.B.I. normally resident in Scotland, in Glasgow on 12th November, at which Dr. Denis Ratcliffe was elected to serve on the B.S.B.I. Council.

At the field meetings, work was directed towards helping the preparation of local floras, the Distribution Maps Scheme and those beginning field botany. Ten members and friends attended at Elgin, 11 at Garth in June, 5 at St. Cyrus, 20 at Duns, 9 at Shetland, and 5 at the Cryptogamic Foray. A proposed meeting at Loch Eil, having attracted only two bookings, was cancelled. Reports of these Meetings will appear in the *Proceedings of the B.S.B.I.* (Vol. 4, Pt. 3).

The Exhibition Meeting at Dundee was attended by about 100 persons. Mr. J. Grant Roger presided in the absence of the Chairman (and spoke briefly about the Committee, the Distribution Maps Scheme and the two Societies). Dr. D. A. Robertson of the Department of Botany, Queen's College, lectured on "The Flora of Angus" and showed many coloured illustrations. He selected for contrast one area on each side of the Great or Highland Boundary Fault which divides the county: *viz.* in the South, the coast at Arbroath, a cultivated area of fertile soil on the Old

Red Sandstone, and in the north, Glen Clova, a Highland region of heather and 'sedge' lying on much older rocks.

The B.S.B.I. official exhibit was displayed together with the following exhibits: (a) Scottish Willows (Miss U. K. Duncan); (a) Wool adventives grown at Forres, Morayshire, in 1958 (Miss M. McM. Webster)—seeds obtained from one lb. of combings from fleeces of Australian sheep from a wool mill in Devon produced plants, nearly all of which set seed although none persisted the following year; interesting plants from Tentsmuir (E. Crapper); (a) wild flower studies, paintings and drawings (L. Fullerton); distribution of Blackberries in Britain, and The Raspberry—wild in Britain (G. Haskell); chromosome instability in *Rubus* (N. N. Tun); a flowering specimen of *Pinguicula grandiflora* (D. A. Robertson); a technique for measuring structural features of plant epidermis using cellulose acetate films (C. North); cellulose destroying fungi; (a) paintings of flowers of the East Lothian coast (Miss Bessie Inglis); plants grown for the Dundee Horticultural Show (R. M. Robertson); residual herbicides (R. J. Stephens); tetraploid mutations in raspberry roots (D. L. Jennings); *Geum macrophyllum* from Kinnordy Loch and aliens from waste ground at Stannergate (H. G. Watson); Botany round the City of Dundee (Miss E. P. Smith); (a) three species of Greater Bindweed (P. S. Green); effect of day length on the physiology of the strawberry (C. G. Gutteridge and P. A. Thompson); plants from Switzerland having Scottish connections (R. Mackechnie); some common woodland fungi found locally (D. A. Robertson); *Carex flava* and its allies and ecological variation in *Juncus bulbosus* (J. L. Colville); the genus *Luzula* in Britain (J. Robertson), and jute trade research (Miss M. Wilson).

The Chairman thanked all the exhibitors and helpers and especially Dr. Edith P. Smith and Dr. and Mrs. D. A. Robertson for their work in bringing about one of the most successful meetings the Committee had held.

In Elgin some 40 people attended and saw those exhibits marked (a) in the foregoing Dundee list together with a herbarium of local Bryophytes shown by Dr. K. Richter of Gordonstoun. Mr. J. Grant Roger gave an illustrated lecture on "The Flora of the Cairngorms". The Honorary Secretary presided, explained the work of the Committee and the sponsoring Societies, and expressed thanks to the Rector of the Academy and to Mr.

Kenneth Wood, Tutor in Extra-Mural Studies at the University of Aberdeen.

In Glasgow the attendance was about 50 and the Chairman presided at the meeting. The following showed colour transparencies of field meetings held during the year: Mr. B. W. Ribbons (Culbin Sands, spoken to by Mr. R. Mackechnie; Loch Loch, spoken to by Dr. D. Ratcliffe; Shetland, spoken to by Mrs. F. M. Elder and Mr. R. Mackechnie); Dr. Denis Ratcliffe (Loch Loch, Cairngorm and Glen Lyon); Dr. F. H. Perring (Dulaw Dene, Berwickshire, spoken to by Mr. R. Mackechnie). Mr. A. McG. Stirling also showed slides taken at Kishorn, Wester Ross and the Mull of Galloway. The following exhibits were shown: plants from Shetland (R. C. Palmer); a new method of preservation and presentation of British Mosses (the Curator, Glasgow Botanic Gardens); some *Equiseta* and two rare species of *Potamogeton* (Miss U. K. Duncan); diet studies of hill sheep (D. J. Martin); Scottish plants in new stations—6 phanerogams, and 2 bryophytes with accompanying descriptions and maps (H. Milne-Redhead); West Ross plants, including new county records (A. Slack and A. McG. Stirling); Culbin plants (J. G. Roger and B. W. Ribbons); Perthshire plants (D. Ratcliffe and B. W. Ribbons); new records from the Isle of Foula (Miss S. C. Holbourn per P. S. Green); plants from the Isle of Colonsay (E. Todd); *Pyrola chlorantha*—a Scottish species? (B. L. Burtt); Shetland plants (Mrs. F. M. Elder, R. Mackechnie and B. W. Ribbons); Berwickshire plants (F. H. Perring); wool, grain, and esparto grass aliens (Miss E. P. Beattie); Carex species from North Swedish Lappland (J. H. Dickson), together with the B.S.B.I. and B.S.E. official exhibits. The Chairman kindly acted as local organiser for this meeting.

Mr. R. Mackechnie was reappointed Chairman, Mr. B. W. Ribbons, Honorary Secretary, and Mrs. F. M. Elder, Field Secretary. Dr. Denis Ratcliffe was co-opted and appointed Meetings Secretary.

The accounts showed a deficit of £13 15s. 5d. for the year 1959, and this amount has been refunded by the two Societies.

During the year the Committee has considered the changes in the B.S.B.I. rules in so far as they affect Scotland and in particular the difficulty of attending Council Meetings in London by

Scottish Members was discussed. At the request of the B.S.B.I. the list of Recorders for Scottish Vice-counties was reviewed. The Committee also noted with pleasure that the Botanical content of the B.B.C.'s Scottish programme appeared to be increasing.

The Secretary once again has pleasure in expressing the Committee's thanks to the officers of the sponsoring societies, the leaders of the field meetings, and the other members and friends who have taken part in the Committee's work during 1960.

B. W. Ribbons, Honorary Secretary.

OBITUARY.

Dr. Dorothy G. Downie.

A native of Edinburgh, Dorothy G. Downie never lost her sense of attachment to the city of her birth and to the family circle of which she was a member. Nevertheless, she was destined to spend the greater part of her life in Aberdeen.

She graduated in Science at the University of Edinburgh in 1917 and two years later earned the distinction of being the first woman in Edinburgh to take a degree in Forestry. To these academic qualifications she added the professional training for teachers at Moray House Training College.

When W. G. Craib was appointed to the Regius Chair of Botany at Aberdeen University in 1920, Dorothy Downie accompanied him as an Assistant. In due course she was appointed to a Lectureship and subsequently to a Readership. A sojourn for three years (1925-28) at the University of Chicago, made possible by the award of a Carnegie Scholarship, brought her under the influence of Chamberlain and provided the opportunity to undertake the research which gained for her the degree of Ph.D. While her investigations were concerned primarily with the problem of fertilization in Cycads (her Ph.D. Thesis dealt with the male gametophyte of *Microcycas calocoma*) she decided also to make a study of Cycads in the field. To this end she spent part of the year 1927 in the Western Sierras of Cuba, collecting material, her journeys frequently accomplished on horseback.

She would probably have remained in America but for an invitation to return to Aberdeen in 1928, and for the next five or six years she carried the main burden of teaching in the Botany Department of the University. It was during this period also that she devoted much time and energy to the improvement of teaching facilities, especially in building up a slide collection. She put the needs of students before everything else and unfortunately her work on Cycads was abandoned.

When research again became possible attention was directed to the problem of Orchid nutrition in relation to the fungal symbiont and *Goodyera repens* was first selected for study. The investigation was soon extended to include other species and D. G. Downie's contributions to the problem of Orchid mycorrhiza,

published in the Transactions of this Society, are a noteworthy addition to our knowledge of this subject. Throughout all her research she practised the most meticulous technique and demanded the same precision and accuracy from students working under her supervision.

Yet her life-work was that of a teacher and as such she will be remembered by generations of students for her clarity of exposition, her ready willingness to help and her unfailing kindness. She remained for nearly forty years a loyal colleague in the Department she served and was an unrivalled leader in the Strathcona Club at Bucksburn where she resided. Owing to illness she retired in March 1960; she died on 22nd August of that year.

J. R. MATTHEWS.

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